

VOL. 37, PART 1

MARCH 1954

The British Mycological Society

(Recognosce notum, ignotum inspice)

TRANSACTIONS

Edited by

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CAMBRIDGE UNIVERSITY PRESS

LONDON: BENTLEY HOUSE, N.W.1

NEW YORK: 32 EAST 57TH STREET, 22

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AQUATIC ASCOMYCETES: DISCOMYCETES FROM
LAKES

By C. T. INGOLD

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(With 15 Text-figures)

An account is given of submerged aquatic Discomycetes growing on reed-swamp plants and water-logged sticks in the English Lake District. The following are recorded and described: *Pachyella depressa* (Phill.) Boud., *Apostemidium guernisaci* (Cr.) Boud., *Belonium excelsius* (Karst.) Boud., *Trichobelonium guestphalicum* Rehm, *Pocillum boltonii* Phill. and *Hypoderma scirpinum* DC. *Apostemidium sporogyrum* sp.n. and *Coleosperma lacustre* gen.n., sp.n. are described.

INTRODUCTION

Dead submerged stalks of reed-swamp plants such as *Schoenoplectus lacustris*, *Eleocharis palustris*, *Typha* spp., *Carex rostrata*, *Phragmites communis*, *Phalaris arundinacea* and *Equisetum fluviatile*, and also, to a lesser extent, submerged water-logged branches of trees, normally bear a fungus flora including species of Fungi Imperfecti (both Hyphomycetes and Sphaeropsidales) and Ascomycetes (both Discomycetes and Pyrenomycetes). Very little is known of them because mycologists interested in Ascomycetes and Fungi Imperfecti have collected almost exclusively in terrestrial habitats and students of aquatic fungi have largely limited their attentions to Phycomycetes. It is a striking fact that no submerged aquatic member of Basidiomycetes has yet been found either in fresh waters or in the sea.

So far as Ascomycetes are concerned, species of Pyrenomycetes are most frequently encountered. Indeed, it is often quite difficult to find a submerged dead reed-stalk free from perithecia. A few of these Pyrenomycetes have already been considered (Ingold, 1951; Ingold & Chapman, 1952), but many of them are still undescribed. The flora of aquatic Discomycetes, with which the present paper is concerned, is small in comparison.

Since the levels of lakes vary with weather conditions, it is natural to inquire if these Discomycetes are truly aquatic or if they are exposed to the air during part of their life. After several seasons' collecting it seems clear that all the species considered below can pass their whole existence below water. Nearly all collecting was done at periods when water-levels were lower than normal, and collections were made at depths varying from several inches to several feet below the surface. Only in *Nipectera pulla* growing on *Phalaris* were apothecia also seen above water-level, and these were dead and shrivelled, having been left high and dry by a falling lake-level.

Aquatic Discomycetes are found in lakes on two distinct substrata: on dead reed-stalks often still *in situ*, and on submerged sticks of trees such as ash, oak and willow. If water-logged twigs and branches are dragged up from the beds of lakes and tarns, apothecia are not infrequently to be found

on them. However, the discomycete flora of submerged dead reeds is much more regular in its occurrence and some species are extremely common (e.g. *Niptera pulla* and *Belonium excelsius*). The aquatic flora of sticks and that of dead reeds are very distinct, and the only species found in both is *Niptera pulla*.

Various species of aquatic Discomycetes are considered below. Some appear not previously to have been described, and in most of the others the structure is imperfectly known.

***Pachyella depressa* (Phill.) Boud.**

This species has been found repeatedly on submerged branches in Windermere, Ullswater, Blelham Tarn and a fish-pond near Wraymires Tarn. Material in all collections was in very good condition and, when the hymenium was examined under the microscope, normal spore discharge from the operculate asci was observed.

The apothecia in most collections were of a date-brown colour, but those from Blelham Tarn were white and thus agree with *P. depressa* var. *pallida* Rea described by Bayliss Elliott (1927). However, it is doubtful if there is justification for recognizing white specimens as belonging to a distinct variety.

This species is easily recognized. The ascus is operculate, the spores oval and the excipulum composed of large roundish cells the outmost of which bear much narrower cylindrical cells with dense granular contents. Mucilage occurs between the loosely arranged hyphae of the hypothecium and also extends as a covering around the whole apothecium (Fig. 1).

At one stage in the development of the ascus, when it is almost full size, the contents present a somewhat peculiar appearance (Fig. 1 B) due to the presence of a large oval, granular mass which looks like a plasmodiophoraceous parasite. Soon, however, this separates into eight almost equal portions which are the young ascospores.

P. depressa is also known as a terrestrial fungus growing on rotten wood in damp places. There is no doubt, however, that it is capable of a completely aquatic existence.

***Apostemidium guernisaci* (Cr.) Boud.**

This has been known for a long time as an aquatic fungus, but its structure has not been fully illustrated. Apothecia were found growing abundantly on a twig submerged to a depth of about a foot in Ullswater. In this material the sessile apothecia vary in size from 0.5 to 1.0 mm. and in colour from pale yellow to deep orange. The hymenium consists of an abundance of asci intermixed with relatively few paraphyses. The asci are very long (360–425 μ), narrow (7.5–9 μ) and cylindrical. The paraphyses are unbranched below, but near their free ends branch several times, the branches intermingling above the tops of the asci to constitute a pronounced epithecium. There is a well-developed subicle (Fig. 2). The structure is very different from that described by Nannfeldt (1932) for *A. fischella*. Each ascus contains a sheaf of very long ascospores (210–320 $\times$ 2–2.5 μ). These are discharged into the water, and on liberation

usually assume a sigmoid form with curvature in more than one plane. The septa cannot be seen in newly liberated living spores, but very soon after discharge most of them disarticulate at the middle point (Fig. 3).

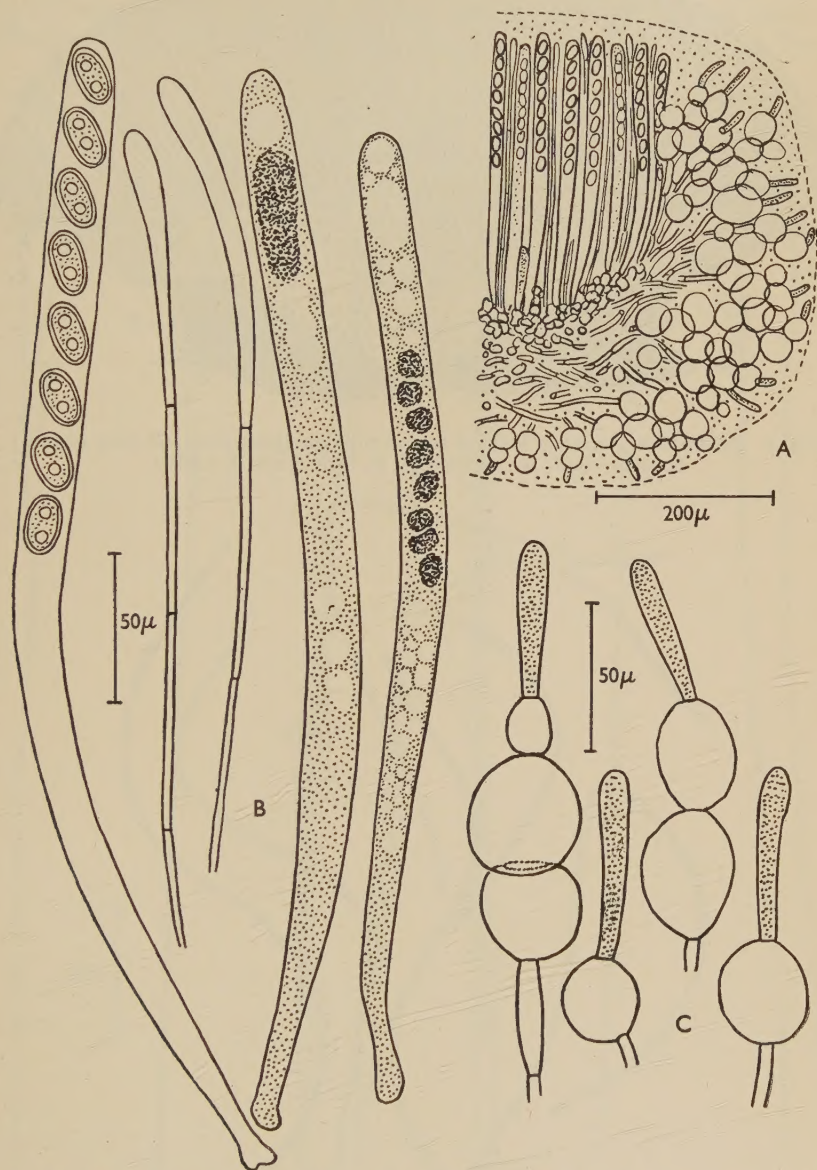


Fig. 1. *Pachyella depressa*. A, marginal part of a vertical section of apothecium; B, asci in various stages of development and two paraphyses; C, hyphae from the excipulum.

The specimens from Ullswater agree very well with Boudier's illustration and with the figures and description of American material given by Durand (1908). However, it is not so clear that they can be identified as

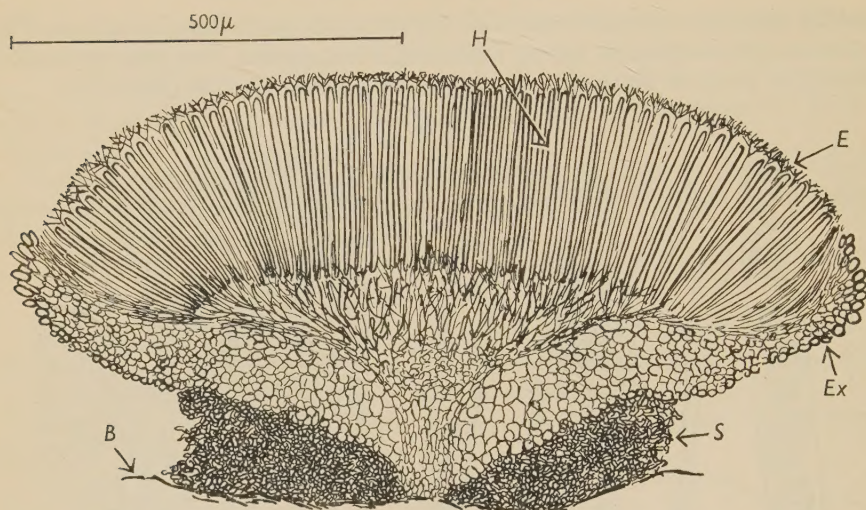


Fig. 2. *Apostemidium guernisaci*. Vertical section through apothecium. *B*, bark of twig; *E*, epithecium; *Ex*, excipulum; *H*, hymenium; *S*, subicle.

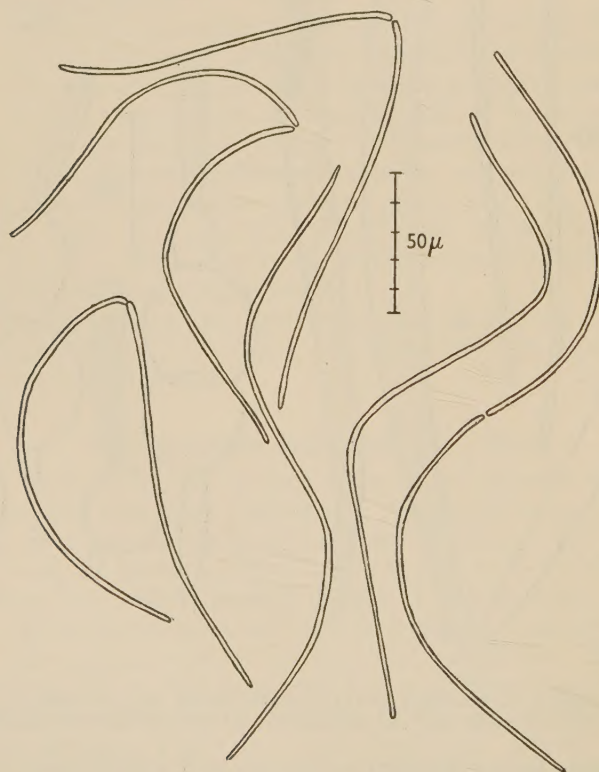


Fig. 3. *Apostemidium guernisaci*. Six freshly discharged spores four of which are disarticulating at the mid-point.

the species (originally *Vibrissea guernisaci*) erected by the brothers Crouan (1857). Their brief description is accompanied by a small picture showing filiform spores $90-110\mu$ long and asci 200μ long which are clavate, not cylindrical. Further, the paraphyses, though branched several times near their free ends, are not otherwise like those shown in Fig. 4. Another



Fig. 4. *Apostemidium guernisaci*. Three asci and five paraphyses.

complication is that the fungus illustrating *V. guernisaci* Cr. in Phillips' monograph of the genus (Phillips, 1881) is clearly wrongly identified. It agrees neither with the original description nor with Boundier's conception of the species.

***Belonium excelsius* (Karst.) Boud.**

This species is very common on dead *Phragmites* stems in Windermere, Esthwaite, Blelham Tarn, Rydal Water and probably in all the lakes of the Lake District. It has also been collected from ponds in Epping Forest and

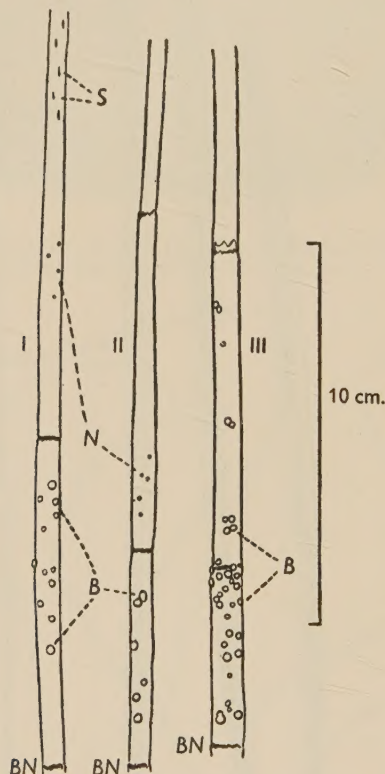


Fig. 5. The basal portions of three dead *in situ* stems of *Phragmites*. I, from Windermere; II, from Blelham Tarn; and III, from Esthwaite. In all the basal node (BN) was submerged to a depth of 2-3 ft. at a time when lake levels were low. B, apothecia of *Belonium excelsius*; N, apothecia of *Niptera pulla* and S, pycnidia of *Stagonospora* sp.

at Esher. It does not occur above water-level on *in situ* stalks, although occasionally it is to be seen on detached stalks cast up on a lake shore. Further, if a bed of *Phragmites* is examined from a boat under bright calm conditions, it is easy to see that the apothecia occur most frequently well below the surface, most often on the basal internode which may be 2-3 ft. below normal lake-level. Very frequently *Niptera pulla* occurs on the same stalks, but although the apothecia of that species may be found at a depth of 2-3 ft., they show no preference for the basal internodes (Fig. 5).

There seems little doubt about the identity of this species. Karsten's type has recently been examined by Dennis (1950), and the Lake District material agrees well with the revised description in his account.

The structure of the apothecium is illustrated in Fig. 6. Although it seems to be seated on a broad base, there is, in fact, a definite stalk. Around this, and filling in the space between the underside of the apothecium and

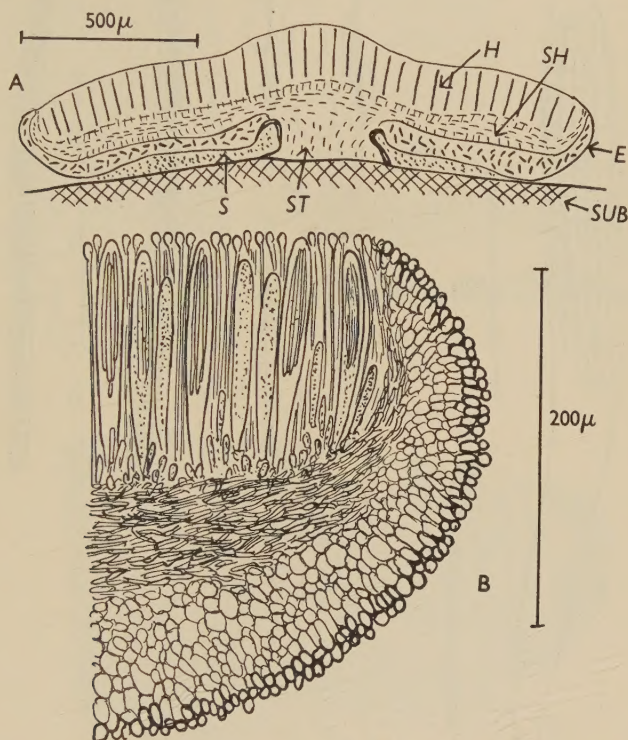


Fig. 6. *Belonium excelsius*. A, diagram of vertical section of apothecium: H, hymenium; SH, subhymenium; E, excipulum; S, subicle; ST, stipe; SUB, substratum. B, marginal part of same apothecium at higher magnification.

the surface of the *Phragmites*, is a poorly defined subicle. The asci (Fig. 7) are cylindro-clavate and the dehiscence pore stains bright blue with iodine. The ascus contains a sheaf of eight spores. A random fifty of these, freshly discharged, had an average length of 70.6μ (extremes: $52.5-92.5\mu$) and an average breadth of 3.2μ (extremes: $2.1-5.0\mu$). The dimensions given by Dennis are $50-80 \times 3-4\mu$. The mature spores were 7- to 10-septate, each cell containing a large number of small oil-globules. Dennis, however, records the spores as 3-septate.

This species appears to be limited to *Phragmites*.

***Trichobelonium guestphalicum* Rehm**

This species was found on submerged dead stalks of *Schoenoplectus lacustris* in Blelham Tarn (August 1951) and on submerged rotting, but

still attached, leaf-bases of *Typha angustifolia* in Esthwaite (July and September 1952). The apothecia (Fig. 8) are small (0.5–1.2 mm. diameter) and greenish grey with a much darker margin. The hymenium consists of asci intermixed with very numerous and very straight simple paraphyses. The asci (Fig. 9) are 160–170 μ long and at their widest 9–10 μ broad. Their

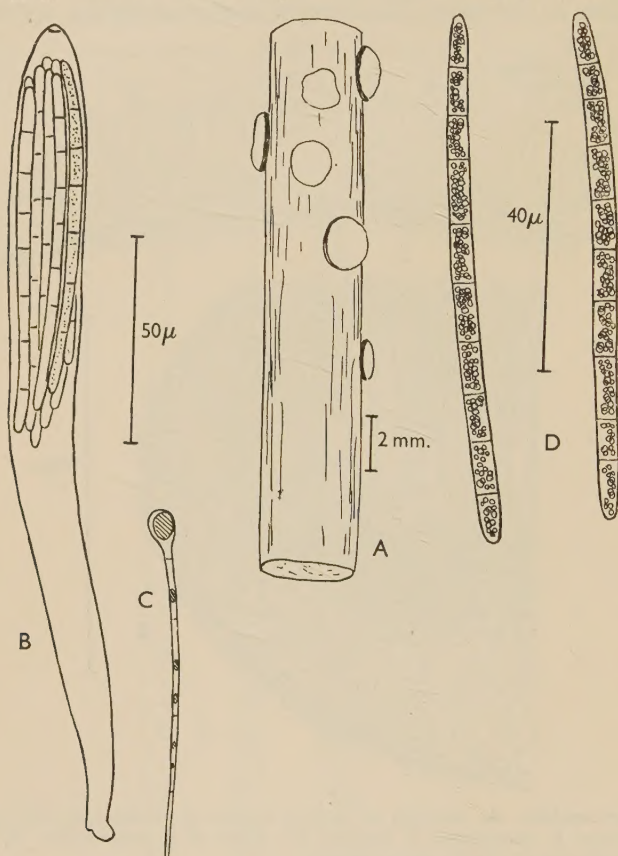


Fig. 7. *Belonium excelsius*. A, portion of *Phragmites* stem with apothecia. B, mature ascus; C, paraphysis; D, spores.

tips are rather pointed in contrast to the bluntness of most asci. The apical pore stains blue with iodine. The spores are long (37–44 μ), narrow (2.5 μ) and usually 3- to 4-septate, the septa being readily visible. The spores are colourless and contain finely granular protoplasm. A marked feature of the Lake District material is the character of the excipulum. Towards the base, in surface view, it is composed of tightly packed spherical cells, but, as the free edge of the excipulum is approached, these give place to elongated cells belonging to hyphae arranged parallel to one another (Fig. 8D).

It is difficult to be sure that this aquatic fungus can be identified as that described by Rehm (1896), but agreement is, perhaps, sufficiently good to warrant the use of the name for the time being.

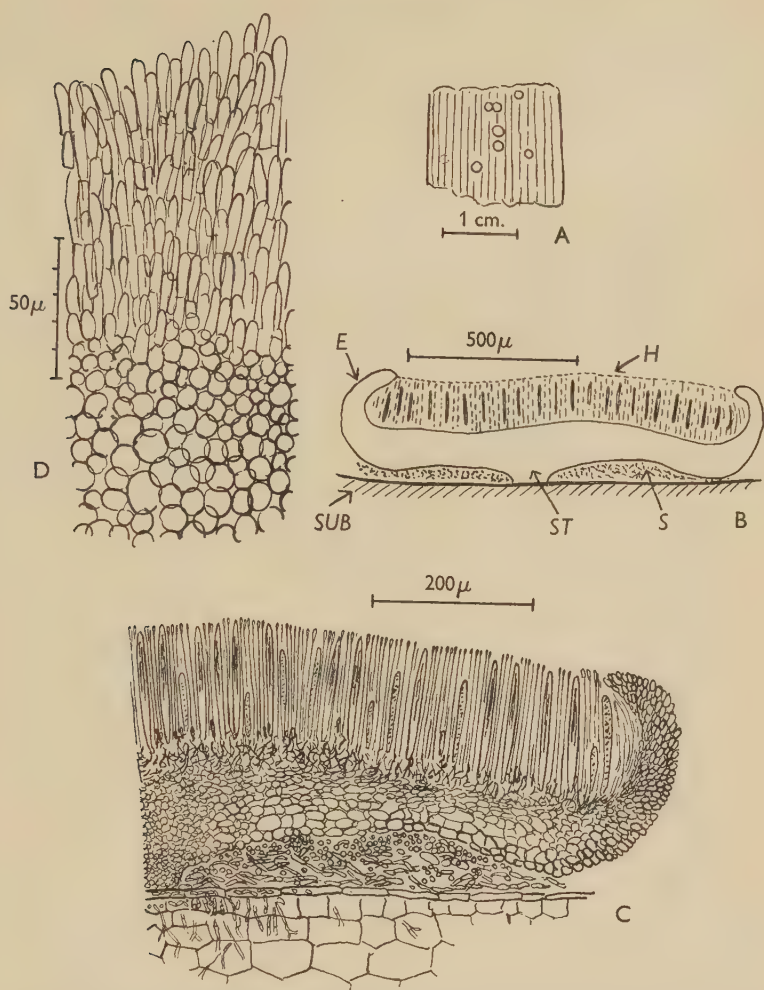


Fig. 8. *Trichobelonium guestphalicum*. A, piece of *Typha* leaf-base with apothecia. B, diagram of vertical section of apothecium: *H*, hymenium; *E*, excipulum; *S*, subicle; *ST*, stalk; *SUB*, *Typha* tissue. C, half of apothecium at higher magnification. D, part of excipulum in surface view.

Coleosperma gen.nov.

Fungi aquatici apotheciis minutis, sessilibus, hyalinis. Ascus octosporus, poro dehiscens. Ascospora in una cellula consistens, lenticularis, paene hyalina, tenui vagina cincta. Typus:

Coleosperma lacustre sp.nov.

Fungus aquaticus apotheciis minutis (0.3–0.5 mm. diam.) sessilibus, hyalinis. Ascus crassus ($140\mu \times 18\mu$), poro apicali dehiscens, octosporus. Ascosporae distichae, unicellulares, lenticulares, $22\text{--}34\mu \times 6.5\text{--}9.0\mu$, guttulas olei plurimas continentes, paene hyalinae. Ascosporae nuper emissae vagina, apicibus apertis, cinguntur.

Hab. In caulibus emortuis, submersis *Schoenoplecti lacustris*, Windermere, Esthwaite et Blelham Tarn, Lancashire, Anglia. Typus: Herb. I.M.I. 51536.

Coleosperma lacustre has been found repeatedly from May to September on dead submerged, but still attached, stalks of *Schoenoplectus lacustris*. It occurs most frequently at depths of 1–1½ ft. and has been collected from Windermere, Esthwaite, Blelham Tarn and Little Langdale Tarn.

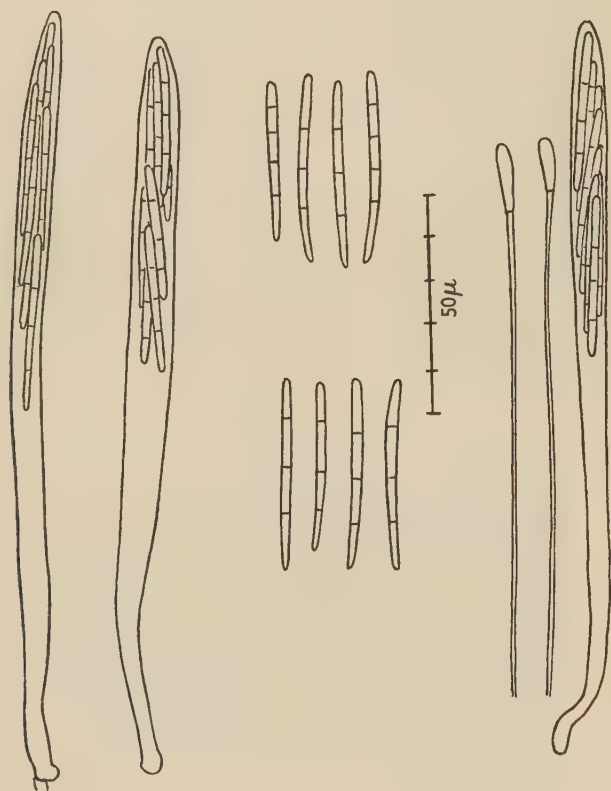


Fig. 9. *Trichobelonium guestphalicum*. Three asci, two paraphyses and eight spores.

The sessile, translucent, white apothecia vary from 0.15 to 0.3 mm. in diameter. The ascus is stout ($140 \times 18 \mu$) and dehisces by an apical pore through which the spores escape singly on discharge. Each ascus contains eight spores arranged roughly in a double row. Each spore is unicellular and lenticular. The average measurements of twenty-five discharged spores selected at random were 27.6μ (extremes: 22.5 and 33.5μ) $\times$ 7.6μ (extremes: 6.5 and 9.0μ). Each spore is crowded with small oil globules except for a small minutely granular region representing the position of the nucleus. The spores are faintly yellow, due to the colour of the oil. The spore-wall is extremely thin. If freshly discharged spores are examined with critical illumination, a delicate sheath can be seen around each. Immediately following discharge this is closed, but very soon afterwards the ends of the sheath appear to dissolve so that the sheath is open (Fig. 10). Both simple and branched paraphyses occur.

This fungus does not seem to have been previously described nor does it fit readily into a known genus. It is, therefore, described as the type species of a new genus.

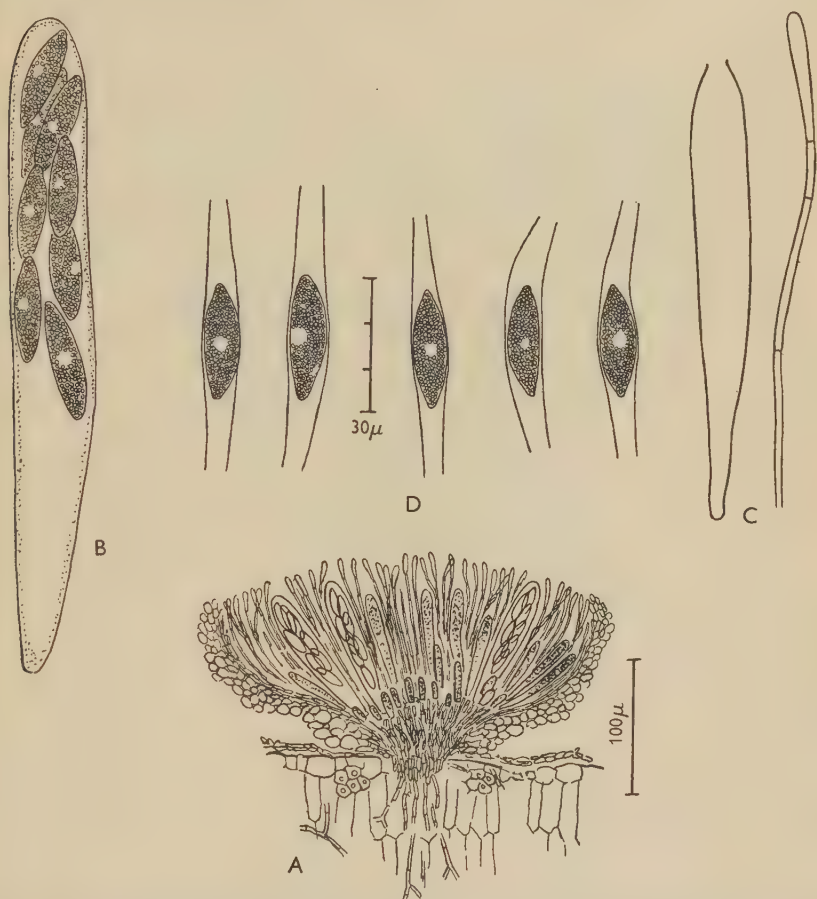


Fig. 10. *Coleosperma lacustre*. A, apothecium in vertical section on *Schoenoplectus*; B, single ascus; C, empty ascus and an unbranched paraphysis; D, five spores.

***Niptera pulla* (Phill. & Keith) Boud.**

Niptera pulla (Fig. 11) is the commonest aquatic Discomycete in the Lake District. It is to be found on a wide variety of submerged dead reed-swamp plants: *Phalaris arundinacea*, *Eleocharis palustris*, *Phragmites communis*, *Juncus articulatus* and *Carex rostrata*. Occasionally it occurs on submerged water-logged sticks. It is, perhaps, most abundant on *Phalaris*. The apothecia are sessile and 0.3–0.8 mm. in diameter. The disk is dark grey, but the excipulum is nearly black. The apothecia are broadly attached to the substratum and there is no stalk as in *Belonium excelsius*, but otherwise the structure of the two species is very similar. The ascus has a pore staining blue in iodine and contains eight colourless ascospores. Fifty freshly

liberated spores, encountered at random, had an average length of 35.4μ (extremes: 29 and 44μ) and an average breadth of 4.1μ (extremes: 3.5 and 5μ). The spore is regularly 3-septate and each cell contains numerous small oil globules.

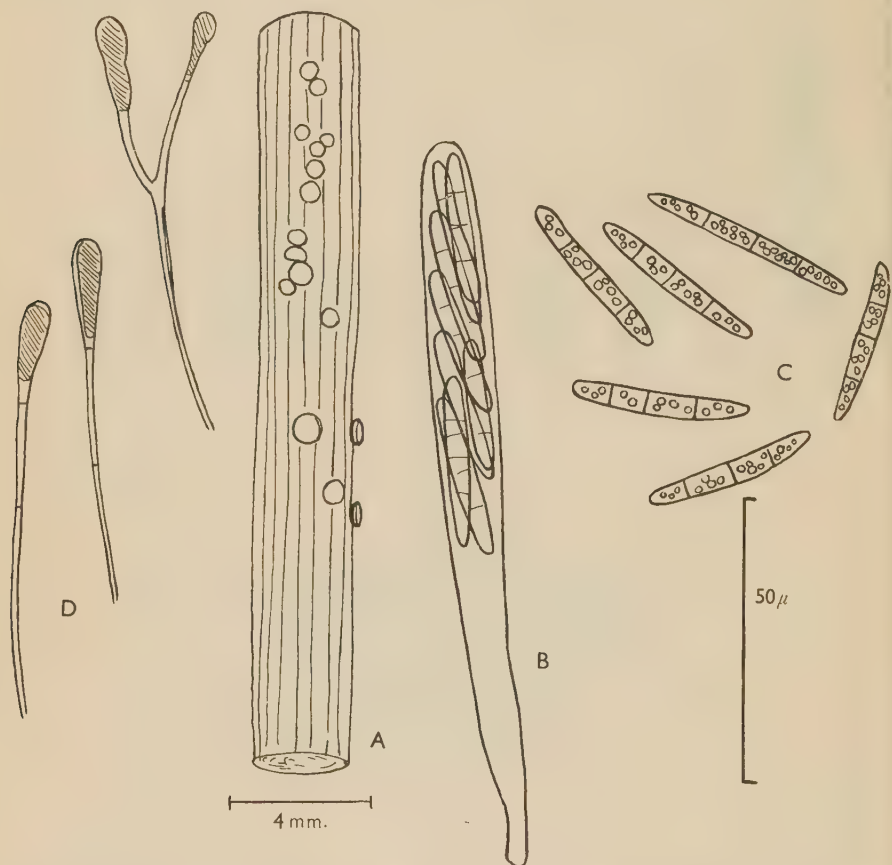


Fig. 11. *Niptera pulla*. A, apothecia on *Phalaris*; B, ascus; C, discharged spores; D, paraphyses.

***Pocillum boltonii* Phill.**

Equisetum fluviatile grows as a reed-swamp plant in lakes usually in clearly circumscribed communities and the erect shoots project into the air whilst their lower parts are continuously submerged. If a horse-tail swamp is examined in summer, a number of stalks are usually to be seen broken short some distance below normal water level. The upper few internodes of these may bear aquatic Ascomycetes including *Pocillum boltonii*. This species was found in June 1951, in Windermere and in Blelham Tarn, and, in August 1951, in Little Langdale Tarn.

The whitish apothecia are minute ($0.2-0.4$ mm. diameter) and occur gregariously on the dead *Equisetum*. The structure of the apothecium is illustrated in Fig. 12. There is a short, stout stalk. The ascus is rather

fusiform ($120-150 \times 18-25\mu$) and contains four long ($75-95 \times 4.5\mu$), colourless ascospores. Each of these has three regions packed with minute oil drops separated by transverse bridges of protoplasm without obvious droplets. Staining shows that a nucleus occurs in both of these bridges so that the unicellular spore is bi-nucleate (Fig. 13).

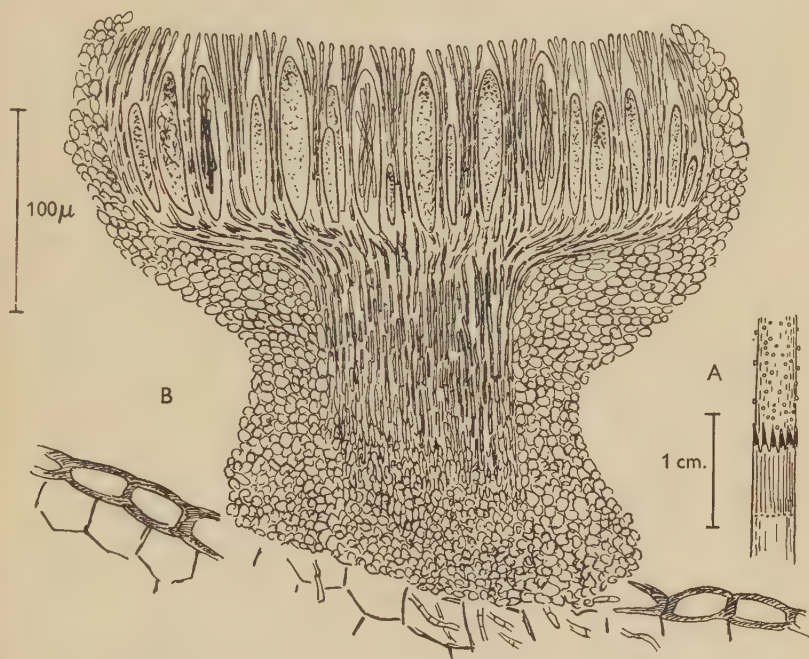


Fig. 12. *Pocillum boltonii*. A, portion of *Equisetum fluviatile* with apothecia; B, section of apothecium.

Pocillum boltonii was originally recorded by Phillips (1887) from submerged stalks of *Equisetum* sp. in the neighbourhood of Birmingham. The asci were described as 8-spored and the spores as $40-50 \times 3-4\mu$. Nevertheless, examination of Phillip's type material in the British Museum (Natural History) shows that the Lake District material agrees with the type which, however, is not in very good condition. The asci of the type appear to be 4-spored and the ascospores are considerably longer ($60-70\mu$) than described. Further, in a pencil drawing attached to the type, the longer ascospores are shown and an ascus is figured with four spores.

Since its original discovery the only record of *P. boltonii* is from south-west Yorkshire (Mason & Grainger, 1937), but no details of this are now available.

***Apostemidium sporogyrum* sp. nov.**

Fungus aquaticus submersus. Apothecium sessile, 0.2-0.4 mm. diam., cineraceum. Asci cylindro-clavati, $170-200\mu \times 12\mu$, dehiscentes poro apicali, I+, octo ascosporas longas in spirae formam convolutas continentes. Ascosporae hyalinae, $125-160\mu \times 3\mu$, 5-7-septatae. Paraphyses infra rectae, supra semel atque iterum ramosae. *Hab.* In caulibus emortuis, submersis *Equiseti fluviatilis*, *Eleocharis palustris*, et *Caricis rostrata*, Little Langdale Tarn, Lancashire, Anglia. Typus: Herb. I.M.I. 51537.

This fungus was found commonly in Blea Tarn and Little Langdale Tarn on submerged dead stalks and leaves of *Equisetum fluviatile*, *Eleocharis palustris*, and, especially, *Carex rostrata*.

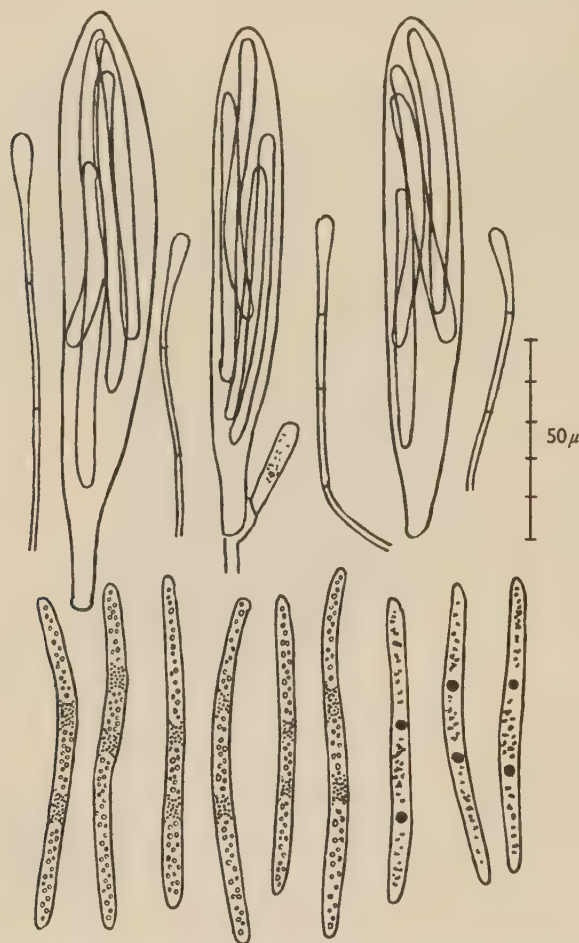


Fig. 13. *Pocillum boltonii*. Above asci three and four paraphyses. Below: nine spores, six on left are from living specimens, three on right are stained to show nuclei.

The apothecia are small (0.2–0.4 mm. diameter) sessile and dark grey with the margin nearly black. In the field it is easy to confuse larger apothecia of this fungus with small specimens of *Niptera pulla* and the two species often occur together on the same substratum. The structure is illustrated in Fig. 14. The asci are 170–200 μ long and 12 μ broad and the dehiscence pore stains blue with iodine. Each ascus contains a sheaf of eight colourless 5- to 7-septate spores, 125–160 μ long by 3 μ broad, twisted spirally together. The discharged ascospores untwist to some extent, but never become completely straight. Spores never seem to lie



Fig. 14. *Apostemidium sporogyrum* on *Equisetum fluviatile*. Above: apothecium in vertical section with cellular details only partly shown; the subicle has separated somewhat from the epidermis. Below: two asci, five spores and a paraphysis.

in a single plane and often assume a sigmoid form. The paraphyses are straight below, but usually branch once or twice towards the free end.

Because of the very long spores, it seems best to place this species in *Apostemidium*, but it should be noted that the spores are not as long and

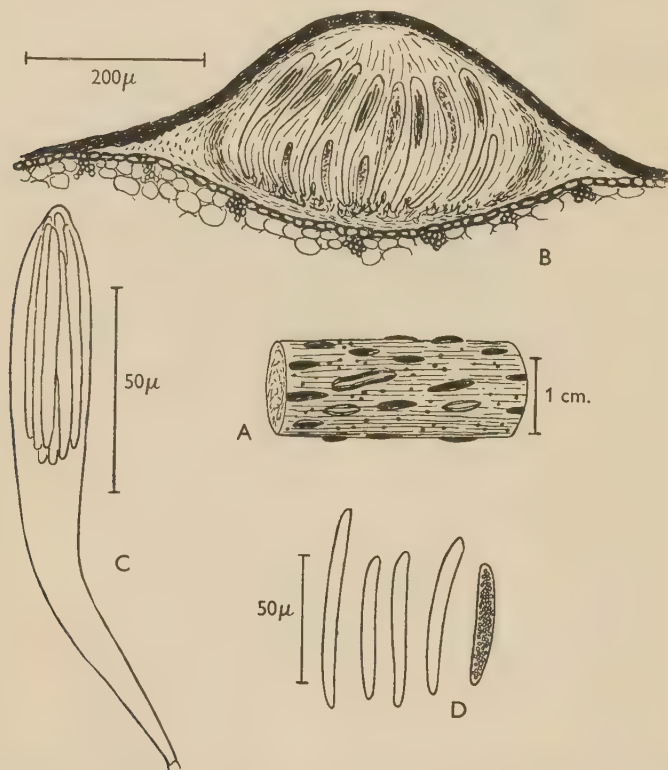


Fig. 15. *Hypoderma scirpinum*. A, portion of a stalk of *Schoenoplectus* with hysterothecia and pycnidia. B, unopened apothecium in vertical section seated on the epidermal cells of the reed. C, ascus. D, ascospores (contents shown only in one).

narrow as in *A. guernisaci*, and the long cylindrical ascus, which seems to be rather an outstanding feature of most species of *Apostemidium*, is not a character of *A. sporogyrum*.

***Hypoderma scirpinum* DC.**

This species occurs, in my experience, on totally submerged parts of dead attached stalks of *Schoenoplectus lacustris*. It was found in quantity in Derwent Water in September 1949, and in Eel Tarn in July 1952. The black hysterothecia occur in large numbers on affected stalks. They are about 0.5 mm. wide and vary in length from 2 to 7 mm. In section it is seen that the hysterothecium is seated on the reed epidermis having arisen, apparently, below the cuticle. The structure is illustrated in Fig. 15 and agrees essentially with Nannfeldt's account (1932). The asci are broad

and clavate, 130–150 μ long, 20 μ broad at the widest part of the ascus which tapers downwards into a rather narrow stalk. The spores are colourless, 50–70 $\times$ 6 μ , unicellular and crowded with small oil globules.

Interspersed with the hysterothecia are small round black pycnidia which probably belong to the same fungus. These contain very numerous minute (1 $\times$ 3 μ) spores which are unicellular and colourless.

GROWTH IN PURE CULTURE

Apostemidium guernisaci, *Belonium excelsius* and *Niptera pulla* have been grown from single ascospores in pure culture on 2% malt agar. All grew readily, but none produced any accessory spores either directly on agar or when strips of agar cultures were submerged in water. Of these three species the only one to fruit in culture was *N. pulla* which produces apothecia on malt agar after about a month at 20° C. It was considered possible that the failure of the other species to form apothecia might have been due to their being heterothallic. However, both in *Apostemidium guernisaci* and *Belonium excelsius* cultures derived from a number of ascospores also failed to fruit. Attempts to bring about fruiting on the sterilized natural substrata immersed in sterile water also failed.

DISCUSSION

The essential point emphasized in this paper is that there is a regular flora of submerged aquatic Discomycetes growing on organic substrata in fresh-water lakes. Although from time to time various aquatic species have been recorded, this particular fungus flora has not previously been recognized as a normal feature of aquatic life in lakes. A consideration of the species described shows that they do not belong to any narrow systematic division in the Discomycetes, Pezizales (e.g. *Pachylla depressa*), Helotiales (e.g. *Belonium excelsius* and *Niptera pulla*) and Phacidiales (e.g. *Hypoderma scirpinum*) are all represented. It is further interesting to note that amongst aquatic Pyrenomycetes the same is true, some fresh-water aquatic forms belonging to Hypocreales (e.g. *Loramyces* spp.) and others to Sphaeriales (e.g. *Ceriospora caudae-suis*). It seems as if the adoption of the aquatic habit has occurred along different lines of evolution, and this indeed is strictly parallel with what has happened amongst flowering plants.

It is of interest to inquire whether these aquatic Discomycetes have any features that suggest adaptation to the aquatic environment. On the whole they are very much like their presumed terrestrial relatives. However, there seems to be a distinct tendency first for the spores to be long and narrow, and secondly for them to be crowded with minute oil drops.

Spore discharge in fresh-water aquatic Ascomycetes takes place much as in terrestrial fungi. The ascus, unlike the basidium, is a spore-gun of a type that can function almost as well under water as in air. In all the Discomycetes considered in this paper the spores appear to be violently discharged just as in terrestrial species, although the distance of discharge is small indeed because the viscosity of water is so much higher than that of air. However, distance of spore discharge is of no significance in aquatic species. All that is necessary is that the spores shall be set free, so that they can be dispersed by water movements.

My thanks are due to Mrs F. L. Balfour-Browne, Dr R. W. G. Dennis and Mr W. D. Graddon for most helpful advice, to Mrs B. Chapman who has cut all the sections necessary for this work, to Professor D. M. Jones for the Latin diagnoses, and to Mr H. C. Gilson for permission to work in the laboratories at Wray Castle and later at Ferry House.

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(Accepted for publication 20 March 1953)

ASCOSPORE FORM

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(With 1 Text-figure)

In most Ascomycetes the lower part of the ascospore is the mirror image of the upper. In many species, however, the upper part is relatively broad and blunt, and the lower narrow and pointed. The reverse arrangement never appears to occur. Possible biological advantages of the ascospore with blunt anterior end and more tapered posterior one are discussed.

In those Ascomycetes (mainly Discomycetes and Pyrenomycetes) in which the spores are violently discharged there is a considerable range of spore size and form. However, in most species, irrespective of size and shape, the upper half (that nearer the apex of the ascus) is usually just like the lower. Thus if a spore is cut transversely at the mid-point of a line joining its extremities, it is thereby divided into two almost equal parts that are mirror images. This type is bipolar-symmetrical. However, in very many species, distributed widely amongst different genera, a transverse cut at the mid-point between the two ends divides the spore into a large relatively blunt upper part and a smaller part with a relatively sharp point. This is the bipolar-asymmetrical type. In such spores the widest part of the spore is nearer the apex than the base. The interesting fact is that the opposite condition never seems to obtain. In looking through the pictures in Berlese's *Icones*, Rehm's *Hysteriales and Discomycetes*, Lorraine Smith's *Lichens* and other monographs, I have been unable to find a species in which a cross-cut at the half-way point would separate the spore into a significantly larger blunt basal part and a smaller, more pointed, upper one.

It is clearly of interest to speculate on what may lie behind this generalization. In such speculation two types of explanation can be put forward: a morphogenic one and a teleological one. They are not mutually exclusive, although a simple morphogenic explanation may suggest that it is superfluous to look for a teleological one. A case in point is the form of birds' eggs. As with ascospores, they may show bipolar symmetry or asymmetry. As in ascospores in the asymmetrical type the blunt end is the anterior one. Here a simple morphogenic explanation is available. This may be quoted from D'Arcy Thompson (1942):

When the egg is subject to the peristaltic contraction of the oviduct during its formation, then from the nature and direction of motion of the peristaltic wave the pressure will be greatest somewhere behind the middle of the egg; in other words, the tube is converted for the time being into a more conical form, and the simple result follows that the anterior end of the egg becomes the broader and the posterior end the narrower.

D'Arcy Thompson points out that the larger the egg in relation to the oviduct the greater will be the effect and the more pointed the eggs. Thus

when a small bird lays a relatively large egg it tends to show bipolar asymmetry, but if the egg is small in relation to the bird it tends to be of the symmetrical type. It is difficult to envisage an explanation of this kind applying to asymmetrical ascospores, since their form is determined whilst they are subject to uniform pressure within the ascus. As there is no obvious morphogenic explanation it is, therefore, of interest to consider a teleological one and to suggest that there is some biological advantage in the asymmetrical spore.

Probably in most Ascomycetes the spores on discharge escape singly, but often the interval between the liberation of successive spores is so brief that discharge of all the eight from an ascus appears to be simultaneous. This is particularly true of species in which the ascus is operculate. In the inoperculate types, in which the ascus dehisces by a very narrow pore, obvious successive discharge is perhaps the rule.

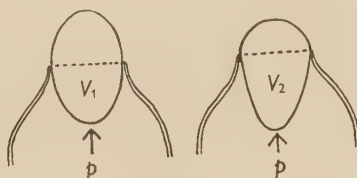


Fig. 1. Spores of the same volume but of different shape, gripped at their widest part by the ascus pore. V_1 volume below dotted line; $V_2 > V_1$; p = hydrostatic pressure.

Consider the escape of a spore from an inoperculate ascus. As the spore is being pushed through the pore and stretching it wider open it will probably be moving very slowly, and when the stretched pore is grasping the spore at its widest part, its velocity is likely to be zero or nearly so. The work done thereafter by the hydrostatic pressure within the ascus is directed towards the discharge of the spore and not towards the stretching of the pore. This work is given by ' pV ' (Fig. 1), where ' p ' is the hydrostatic pressure within the ascus and ' V ' is the volume of that part of the spore immersed in the ascus sap at this stage, and, assuming the friction between spore and pore to be of relatively small magnitude, this can be equated to $\frac{1}{2}mv^2$, where ' m ' is the mass of the spore and ' v ' its initial velocity on discharge. It is quite clear that for spores of equal mass the nearer the widest part is to the front end, the greater V and, therefore, all else being equal, the greater the initial velocity and hence the distance of discharge.

Quite apart from the effect suggested above, the spore with bipolar asymmetry is to some extent stream-lined. Air resistance is reduced as compared with a symmetrical type of equal mass and the distance of discharge is thus increased.

There is some evidence to suggest, however, that the advantage of the asymmetrical type is principally concerned with the escape of the spore from the ascus rather than with its flight through the air. In the operculate Discomycetes the opening of the ascus is relatively wide. Thus the gripping effect of the pore on the spore is slight, and little work is probably required to stretch the pore so that the ascospore can escape. Here the advantage

of the asymmetrical type would seem to be greatly reduced, and in fact all operculate Discomycetes appear to have spores of the symmetrical type. Again in those Pyrenomycetes where the spores are very small, they would seem always to be bipolar-symmetrical. This is true, for example, throughout the Allantosporae.

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(Accepted for publication 14 February 1953)

A CORRECTION

A mistake unfortunately escaped correction in my 'Studies on larch canker. I. The taxonomy and biology of *Trichoscyphella willkommii* (Hart.) Nannf. and related species', *Trans. Brit. mycol. Soc.* **36**, 362-374, 1953.

The ascus measurements for *T. willkommii* are incorrect—the figures for *T. hahniana* having been given instead. The correct figures (p. 367, lines 15-16) are: $127-180 \times 9-12\mu$, mostly $135-165 \times 9.5-11\mu$ (instead of $90-156 \times 9-12\mu$, mostly $105-130 \times 9.5-11\mu$.) The ascus length is one of the diagnostic features used in separating the two species.

J. G. MANNERS

APHANOMYCES DAPHNIAE SP. NOV., PARASITIC ON DAPHNIA HYALINA

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(With 3 Text-figures)

Aphanomyces daphnia sp. nov. was found parasitizing *Daphnia hyalina* var. *lacustris*. Filamentous zoosporangia emerging through the wall of the host were of typical *Aphanomyces* type, with a single row of zoospores encysting immediately on emergence. Oogonia were abundant in some specimens, each with a single egg and 1-3 declinuous antheridia. Parasitism was confirmed by infection experiments on *Daphnia*, and it was found not to parasitize other crustaceans occurring with the *Daphnia*. The fungus was easily cultured on oatmeal agar, and this culture material was used for further infection experiments. The zoosporangia of the culture were more vigorous than those of the naturally occurring material, and under the higher temperatures of the laboratory the zoospores often swam away on emergence, behaving like those in *Leptolegnia*. Oogonia and antheridia in culture material differed only slightly from those in natural material.

Aphanomyces daphniae sp. nov.

Hyphae non septatae, ramosae, 10μ latae, intra hospitem ramificatae. Zoosporangia e pariete hospitali orthogonie ortis, $150-200\mu$ longis, 10μ latis, acute ad 5μ in ove deminutis, in eo puncto constrictis ubi per parietem hospitali emergunt, aliquando breves ramos lateralis $8-12\mu$ longos portantibus.

Zoosporis primis uno ordine formatis, in racemo cystorum apud os vel zoosporangia vel rami lateralis in ipso puncto temporis emergentiae collectis. Cystis 18μ in diam., zoosporis secundariis reniformis, biflagellatis, flagellis equilongis, flagello quoque 15μ longo, lateraliter alligato.

Oogoniis post zoosporas liberatas formatis, $36-38\mu$ in diam., pariete levi $1.0-1.5\mu$ lato singuloque ovo $33-35\mu$ in diam.; olei guttulis in medio ovo in globum incompositum collectis. Caulibus plerumque ramis lateralibus brevibus hypharum primarum 8μ latis, nonnumquam tumidis.

Antheridiis simplicibus, $15\mu \times 18\mu$, ab hyphis remotis ortis id est declinibus. 1-3 ad oogonium quodque indiscriminatum applicatis.

Habitatione parasitica in *Daphnia hyalina* var. *lacustris*, ex Loch Dunmore, Pitlochry, Scotland.

Type slide and culture of the fungus have been deposited at the Commonwealth Mycological Institute, Kew, under no. I.M.I. 50699.

The fungus was first found in the summer of 1950 infecting specimens of *Daphnia hyalina* var. *lacustris* taken from a plankton trap in Loch Dunmore, Pitlochry, Perthshire. Some specimens were so heavily infected as to be covered by a conspicuous 'fur'. In 1951 living specimens of the infected crustacean were collected by means of a plankton net, and from some of these the fungus was isolated on oatmeal agar, on which it grows well.

In the field specimens the non-septate hyphae form a branching system within the body of the host, the width of these internal hyphae varying

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from 10 to 20 μ . Arising from hyphae running parallel to and just within the wall of the host, zoosporangia grow out vertically to a distance of 150–200 μ . Each zoosporangium is about 10 μ wide throughout its length, except where it penetrates the host wall, where it is constricted. At the mouth it tapers sharply to about 5 μ wide. Short side branches are formed, 8–12 μ in length on some of the zoosporangia (Fig. 1*a, b*). The zoospores are formed in a single row, encysting at the mouth of the zoosporangium immediately on emergence (Fig. 1*c, d*); occasionally zoospores may emerge through the short side branches. Each cyst is about 18 μ in diameter, giving rise to a single reniform zoospore which emerges through a pore in the wall of the cyst. The two flagella of the secondary zoospore are equal in length, 15 μ , and laterally attached, one pointing forward and the other trailing behind.

Oogonia are formed after the zoospores are liberated, and in some specimens of *Daphnia* examined were so abundant as almost to fill the body cavity. Each oogonium measures 36–38 μ in diameter, with a smooth wall 1–1.5 μ thick, and contains a single, slightly granular egg, 33–35 μ in diameter. There is no well-defined oil globule in the oospore, but small drops tend to collect in an irregular mass at the centre. Most of the oogonia are borne on short laterals 8 μ thick, but sometimes the oogonial stalks are irregularly swollen (Fig. 2*a*). The antheridia are simple, swollen, 15 $\times$ 18 μ , declinous in origin, arising from distant hyphae. There are 1–3 antheridia to each oogonium, the application being indiscriminate (Fig. 2*b*).

The fungus was isolated by washing a heavily infected *Daphnia* several times in sterile water, and placing it on a plate of oatmeal agar. The initial growth was slow, with branching hyphae radiating from the centre of inoculation, varying little from 10 μ in thickness throughout the culture. No aerial hyphae were formed in the original culture, and they were sparse in later subcultures, the mycelium remaining embedded in the culture medium. The subcultures from the original isolate have so far remained true to character. When a small piece of culture material is placed in water, growth is more rapid, but somewhat irregular, the thickness of the hyphae often varying from 15 μ at the proximal region to 6 μ at the distal parts. Many of the hyphae show a slight spiral formation, a condition which has been described for other species of *Aphanomyces*.

The formation of zoospores is erratic, frequently not taking place until an extensive web of hyphae has grown out from the original piece of agar culture, but the introduction of one or two *Daphnia* seems to quicken the process. Usually a complete hypha is transformed into a zoosporangium, the zoospores forming a single row of rod-shaped bodies. At first they are joined to each other by fine threads of protoplasm, but when the zoospores separate these appear to be withdrawn (Fig. 1*e*). Careful observation under oil immersion has revealed that these threads are double (Fig. 2*f*) and it is possible that they are the precursors of flagella.

Zoospores are liberated most frequently at night, and, if the temperature does not rise above 18° C. during liberation, the zoospores immediately encyst at the mouth of the zoosporangium. In the laboratory the daytime temperatures often rose to above 20° C. as there was no temperature control. Under these conditions zoospores on emerging swam away before

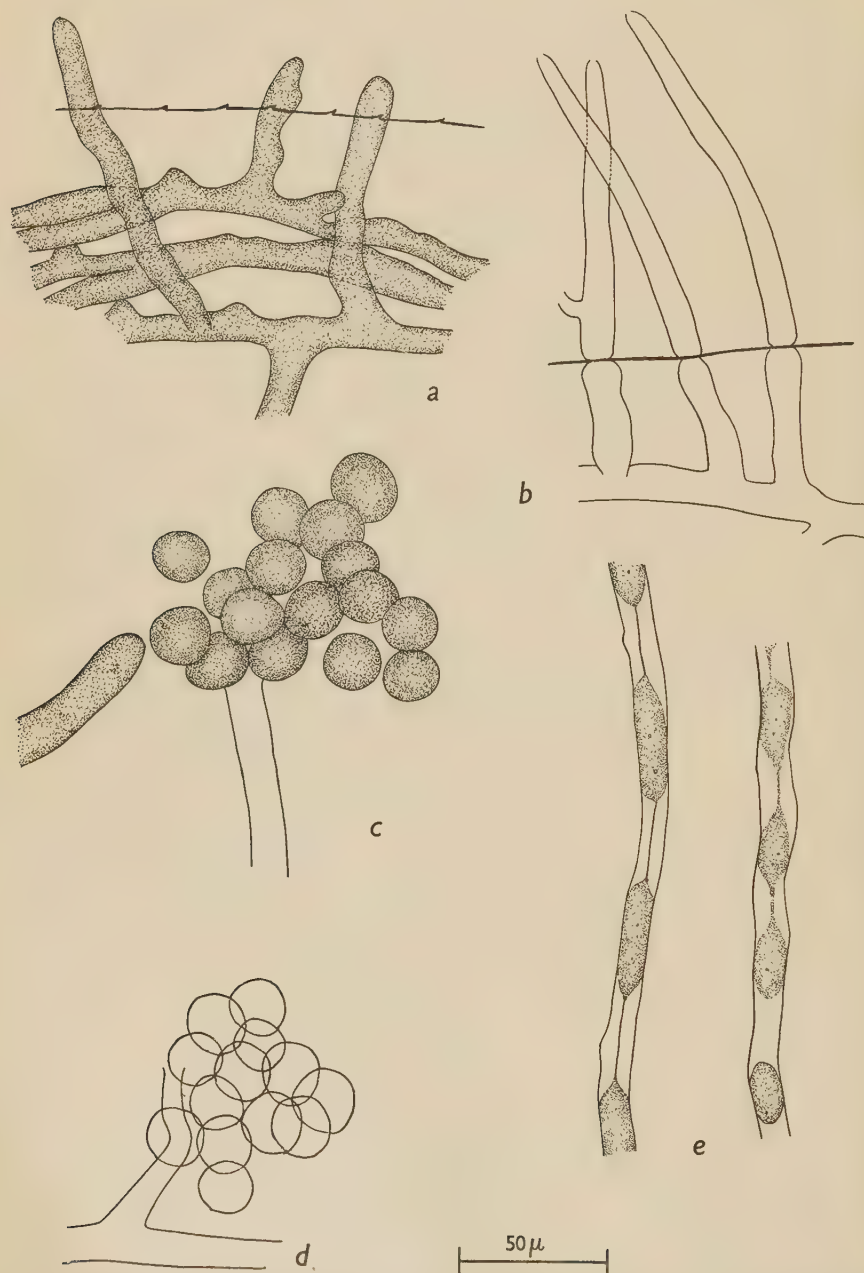


Fig. 1. Formation of zoosporangia and zoospores in *Aphanomyces daphniae*: (a) zoosporangia branching from hypha within the wall of *Daphnia*; (b) empty zoosporangia showing the constrictions and a lateral branch; (c) encysted zoospores; (d) empty cysts; (e) zoospores forming inside the zoosporangium.

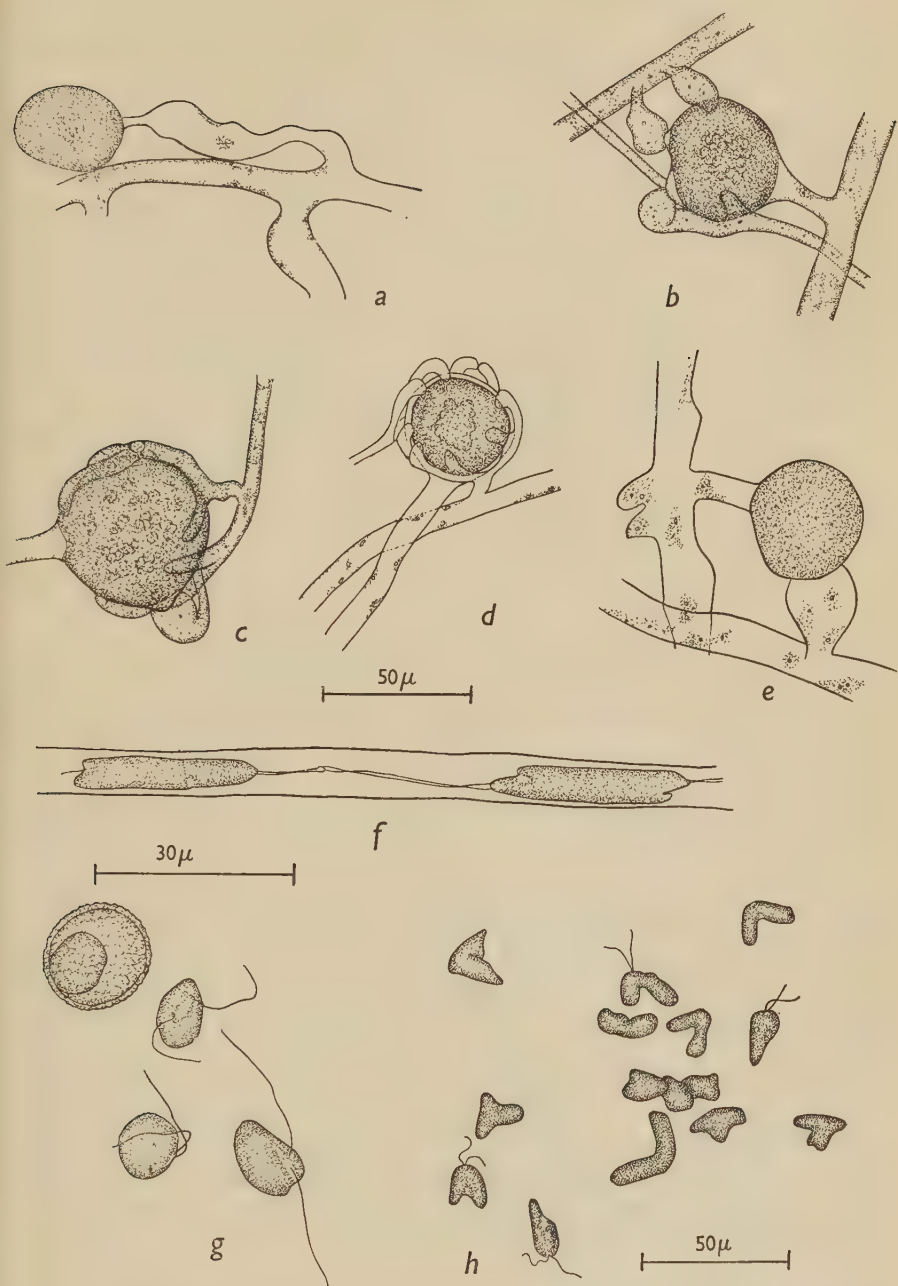


Fig. 2. *Aphanomyces daphniae*: (a) an oogonium with a swollen stalk; (b, e) oogonia and antheridia as seen in collected specimens of infected *Daphnia*; (c, d) oogonia with branched antheridia as seen in culture material; (f) zoospores within the sporangium, showing the double connecting thread of protoplasm; (g) secondary zoospore and a cyst containing a single zoospore about to emerge; (h) primary zoospores which have emerged without encysting.

encysting. Each zoospore emerged as a rod-shaped body $20-30\mu$ long, which immediately bent about its mid-point to form an arrow-head, from the apex of which two equal flagella $12-15\mu$ in length pointed forward. This suggests that the double thread seen in the zoosporangium may have been attached midway along the rod-shaped zoospore. While still swimming the zoospore then became triangular and finally pyriform before encysting, the whole operation from emergence to encystment occupying 10-15 sec. (Fig. 2*h*). After 4-6 hr. a typical secondary zoospore emerged from the cyst through a well-marked pore, each zoospore being reniform, isokont, the flagella being 15μ in length and laterally attached (Fig. 2*g*). In field specimens of *Daphnia*, where the zoosporangia rarely exceed 200μ in length, the number of zoospores encysted at the mouth of each sporangium is usually 10-30. In culture material, under the warmer conditions of the laboratory, the zoosporangia are often 2 mm. or more in length, and as many as 200 zoospores may be liberated from each sporangium.

Oogonia and antheridia are easily induced on agar culture material in water by placing half a sterile hemp seed with the cut surface downwards on the agar. After 24 hr. large numbers of sexual organs develop round the hemp seed, the oogonia differing little from those found in field specimens of infected *Daphnia*. The antheridia, however, are often narrower, 7-10 μ wide, and branched (Fig. 2*c*, *d*).

Experiments on artificial infection

By transferring a living specimen of *D. hyalina* var. *lacustris*, well-washed with sterile water, to a dish of water containing a freely sporing culture of *Aphanomyces* it was found easy to infect the crustacean. The first zoospore of the fungus had settled on the carapace of the host and had begun to penetrate within 3 sec., and was quickly followed by others (Fig. 3*c*). At the end of 8 hr. the host was dead and an extensive mycelium was growing inside. Even with as few as five zoospores present infection took place, although the time taken was longer, 5-10 min. In every case penetration was through the chitinous wall of the host, and although zoospores were swept up in the gut of the animal, they did not seem to germinate. Specimens of *Daphnia* killed by boiling were so heavily covered with zoospores that the resultant mycelium was weak and thin through their competitive growth. From the above experiment it was quite evident that the fungus was an active parasite of *D. hyalina* var. *lacustris* but attempts to infect the crustaceans *Eurycercus*, *Bosmina*, *Diaptomus* and *Cyclops*, were all unsuccessful, and these were never found parasitized in the field, not even in dead specimens, which however were often infected with *Saprolegnia*. Other species of *Daphnia* were not available at the time to test whether the fungus would parasitize them, but it seems at least probable that the fungus is confined to species of *Daphnia*.

The occurrence of hyperparasitism

Close examination of preserved specimens of *Daphnia*, especially using phase contrast, revealed the presence of a second species of *Aphanomyces* apparently parasitic on the first (Fig. 3*d*). No sexual organs were seen in this second species, but measurements of the hyphae, $2.5-4\mu$ wide, and of

the zoospores $4-5\mu$ in diameter, suggest that it might be *A. parasiticus*, usually found attacking *Dictyuchus* and *Achlya*. Without living material however, it is not possible to check the identification.

Systematic position

There seems no doubt that the parasite of *Daphnia* described above should be placed in the genus *Aphanomyces* by virtue of its single row of zoospores encysting on emergence at the mouth of the zoosporangium.

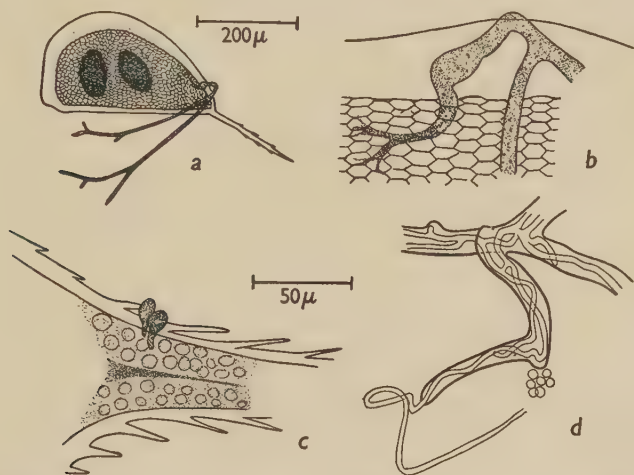


Fig. 3. *Aphanomyces daphniae*: (a) ephippium of *Daphnia* attacked by the fungus; (b) the same under high power; (c) zoospores germinating and penetrating the wall of an adult *Daphnia*; (d) *Aphanomyces parasiticus* growing inside *A. daphniae*.

The fact that under the warmer conditions of the laboratory the primary zoospores may swim away before encysting merely serves to show that the distinction between *Aphanomyces* and *Leptolegnia* may not be very marked. *Aphanomyces* may be regarded as having been derived from *Leptolegnia* by suppression of the primary stage. Only under abnormal conditions does it revert to the biplanetic state.

Within the genus *Aphanomyces* the ornamentation of the oogonial wall may range from completely smooth to very spiny. *A. daphniae* has smooth-walled oogonia and shows some resemblance to *A. laevis*, which it approaches in size. In *A. laevis*, however, the oospore is distinctly hyaline (not granular as in *A. daphniae*) and there is a single well-marked oil globule (in *A. daphniae* the oil drops form an irregular central mass). A more marked difference is that *A. laevis* is saprophytic on insect exuviae, whereas *A. daphniae* is parasitic, apparently confined to *Daphnia*, and could not be cultured on insect exuviae. It therefore seems justified to describe it as a new species and because of its host range the epithet *daphniae* seems appropriate.

Allied fungi parasitic on crustacea

Although the genus *Aphanomyces* includes both saprophytic and parasitic species, only three species have so far been reported as being parasitic on Crustacea. These are *Aphanomyces ovidestruens* Gicklhorn, parasitic on *Diaptomus* (Gicklhorn, 1923), the present species on *Daphnia*, and *Aphanomyces astaci* Schikora on *Astacus*. The latter has been responsible for serious epidemics from time to time, apparently destroying whole populations of *Astacus* (Rennerfelt, 1936), and Benisch (1940) has been able to infect artificially *Eriocheir sinensis* with the same fungus.

The closely allied genus *Leptolegnia* also includes parasites of Crustacea. *Leptolegnia caudata* de Bary has been reported as an important parasite of *Leptodora* (Petersen, 1909), while more recently a closely allied species has been reported as causing epidemics in the copepod *Eurytemora hirundoides*, so serious as to clog the herring nets (Vallin, 1951). Apparently it is confined to this species of copepod. *Daphnia* itself has been reported as being parasitized by *Pythium daphnidarum* (Petersen, 1909), and the curious *Amoebidium* is a frequent parasite. Couch (1942) has described a species of *Lagenidium*, *L. callinectes* parasitic on the eggs of the blue crab *Callinectes sapidus* Rathburn.

My thanks are due to Mr Donald Scott, late of the Brown Trout Research Laboratory, Pitlochry, for first bringing the fungus to my notice. To Prof. C. T. Ingold of Birkbeck College I must express my gratitude for all the helpful advice and criticism he has given me in connexion with these studies, and to Mr Michael Barbour of University College, Khartoum, I must express my thanks for the Latin diagnosis. Thanks are also due to the Scottish Home Department and the Brown Trout Research Laboratory for facilities to carry out this research, and for permission to publish these results.

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(Accepted for publication 10 February 1953)

GLOEOTINIA—A NEW GENUS OF THE SCLEROTINIACEAE

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The new genus is based on *Sclerotinia temulenta* (*Phialea mucosa*), the fungus which causes the blind-seed disease of rye grass; it is placed in the Sclerotiniaceae. It differs from all the genera of this family and from the Phialeoideae in its conidia embedded in mucilage, the character of the stroma and the anatomy of the apothecium.

Endoconidium temulentum, a fungus parasitic on rye, was described by Prillieux & Delacroix in 1891. The name was chosen on account of the mode of development of the spores, which have now been identified as spermatia (microconidia). The name *Phialea temulenta* was given by the same authors in 1892 to the perfect stage of this fungus. In 1893, the fungus was transferred to *Stromatinia* (Prillieux & Delacroix, 1893), at that time regarded by the French mycologists as a subgenus of *Ciboria* (Boudier, 1885) and became *Ciboria* (*Stromatinia*) *temulenta*. The change was based on the nature of the sclerotium, or rather, of the condensed stroma which took its place (Prillieux, 1897).

Rehm described the rye fungus independently in 1900 and assigned it to *Sclerotinia*, as *S. secalicola*. When Boudier gave *Stromatinia* the rank of genus in 1907, he called Rehm's species *S. secalicola*. The two fungi on rye were shown to be identical (Saccardo, 1906; Rehm, 1915) and were named *Sclerotinia temulenta* (Prill. & Delacr.) Sacc. & D. Sacc.

The 'blind-seed' fungus, described on *Lolium perenne* by Neill & Hyde (1939), was tentatively assigned by them to *Helotium*. Its conidial stage somewhat resembles that of *H. herbarum*. Wilson, Noble & Gray (1940) drew attention to the fact that in the blind-seed fungus, as in *Phialea temulenta*, the spermatia (microconidia) are developed endogenously. The only important difference was, at that time, that macroconidia had not been described for *P. temulenta*.

Since it was not possible, during the war-years, to obtain material of *P. temulenta* for comparison, the blind-seed fungus was provisionally named *P. mucosa* (Gray, 1942). According to Nannfeldt's classification based largely on the anatomy of the apothecium (Nannfeldt, 1932), the blind-seed fungus agreed with *Phialea* rather than with *Helotium*, *Sclerotinia*, *Stromatinia* or *Ciboria*.

Neill & Hyde (1942) established the identity of the blind-seed fungus with *Phialea temulenta* when they reported macroconidia, indistinguishable from those of the blind-seed fungus, on the rye grains on which Prillieux and Delacroix based their description.

The rediscovery of *P. temulenta* revived the problem of its taxonomy. There were some grounds for erecting a new genus based on the macroconidial stage, in the manner of Whetzel and his associates, but this seemed premature while so little was known about conidial stages in other species of *Phialea*.

With the publication of the works of Whetzel (1945) and Buchwald (1947, 1949), the relationships of many species within the Helotiales have been greatly clarified. The family Sclerotiniaceae, according to Whetzel (1945), is characterized by stromata, stipitate apothecia, ellipsoidal ascospores and globose spermatia. He regarded the development of a stroma as 'the most outstanding mark of their natural relationship' and laid great stress on the form of this organ as a basis of classification. Discussing the occurrence of a conidial stage, he wrote: 'I have not as yet discovered a case in which this feature fails to be correlated with the type of the stroma.'

Buchwald worked in Denmark on similar lines to Whetzel. He did not, of course, see the American literature until 1945. His diagnosis of the family Sclerotiniaceae resembles that of Whetzel but lays more stress on the anatomy of the apothecium, particularly the presence of a well-defined excipulum, as a diagnostic character.

Seaver (1951), in suggesting that *Sclerotinia temulenta* should be made a separate genus on account of its imperfect stage *Endoconidium temulentum*, did not apparently realize that this latter name describes the spermidial stage which is characteristic of many members of the Sclerotiniaceae.

The blind-seed fungus, *Phialea temulenta*, exhibits certain of the features of the Sclerotiniaceae as described by Whetzel (1945) and Buchwald (1949). It possesses a stalked, cupulate, fleshy apothecium which arises from a stroma. The ascospores are ellipsoidal and spermatia of a type found in members of the family are produced. There is a macroconidial stage.

P. temulenta differs from members of the Sclerotiniaceae in two important characters. The stroma, which is composed of hyphae ramifying in the tissues of the caryopsis, does not show the degree of differentiation found in the genera described hitherto. The anatomy of the apothecium differs from that usually found in the family. In the majority of the Sclerotiniaceae, there is a distinct excipulum (Nannfeldt, 1932), composed of short-celled hyphae which terminate at right angles to the surface. This layer is not present in the apothecium of *P. temulenta*, which is very uniform in structure, composed throughout of slender hyphae, lying parallel to the surface (Gray, 1942).

On the basis of the parasitic habit, type of life history and the presence of spermatia and macroconidia, there is doubtless more justification for placing *P. temulenta* in the Sclerotiniaceae than for retaining it in the Phialeoideae. The macroconidia of *P. temulenta* differ from those associated with any existing genus. Whetzel and his fellow workers have established the practice of basing genera within the Sclerotiniaceae on the macroconidial stage. In consequence we are reluctantly obliged to erect a new genus, with *P. temulenta* as the type species.

The name *Gloeotinia* has been chosen because of the slimy nature of the conidia, a distinctive character of the blind-seed fungus.

GLOEOTINIA gen. nov.

Genus hoc novum spermatiis una cum conidiis praesentibus, habitu parasitico, potius cum Sclerotiniaceis quam cum *Phialea* affinitatem praebet; a *Ciboria* conidiis praesentibus, structura apothecii homogenea divergit.

Stroma ex hyphis septatis intertextis, ad mures paululo incrassatis compositum, per matricem invasam ramosis, in corticem et parenchyma medullare haud discretum, faciem superficiale vix commutans.

Spermidium in forma spermodochii; spermatia globosa, primaria constrictione sub apice spermatiphorae conficta, cetera in serie regulari intus tubum ex parte spermatiphorae terminali constituta.

Conidia unicellularia, cylindrica ad allantoidea, hyalina, numerosissima, ex apicibus ramulorum mycelii aerii brevium exeuntia atque muco commixta.

Apothecia carnosa cupularia stipitata; structura omnino plus minusve homogenea; excipulum haud clare definitum; asci cylindrico-clavati, foramine non iodo caerulescentibus; ascospores laeves unicellulares ellipsoideae hyalinae; paraphyses filiformes.

Type species: *Gloeotinia temulenta* (Prill. et Delacr.) comb. nov.

Synonyms:

Status ascophorus

Phialea temulenta Prill. & Delacr. (1892), pp. 22-23.

Ciboria (*Stromatinia*) *temulenta* (Prill. & Delacr.) Prill. & Delacr. (1893), p. 200.

Stromatinia temulenta (Prill. & Delacr.) Prill. & Delacr. in Prillieux (1897), pp. 453-459; Boudier (1907), p. 109.

Sclerotinia secalincola Rehm (1900), p. 192.

Sclerotinia temulenta (Prill. & Delacr.) Sacc. & D. Sacc., Saccardo (1906), p. 42.

Stromatinia secalincola (Rehm) Boud. (1907), p. 109.

Phialea mucosa Gray (1942), pp. 329-333.

Status microconidiophorus

Endoconidium temulentum Prill. & Delacr. (1891), pp. 116-117.

Stroma not differentiated into rind and medullary parenchyma, not altering the outward appearance of the organ parasitized; composed of septate intertwining hyphae which have slightly thickened walls and ramify throughout the tissues.

Spermidium a spermodochium; spermatia globose, the first formed by a constriction below the apex of the spermatiphore, the rest developed in succession inside a tube formed by the terminal portion of the spermatiphore.

Conidia unicellular, cylindrical to allantoid, hyaline, developed in very large numbers, in succession, from the apices of short outgrowths of the aerial mycelium, forming a slime.

Apothecia fleshy, cupulate, stalked; structure comparatively homogeneous throughout; excipulum not clearly defined; asci cylindrical—clavate, the pore not staining blue with iodine; ascospores smooth, unicellular, ellipsoidal, hyaline; paraphyses filiform.

In possessing spermatia and conidia, and in the parasitic habit, this genus shows more affinity with the Sclerotiniaceae than with *Phialea*. It differs from *Ciboria* in having conidia and in the structure of the apothecium being homogeneous.

Specimens have been deposited at: the Royal Botanic Garden, Edinburgh, the Royal Botanic Gardens, Kew, the Commonwealth Mycological Institute, Kew, the British Museum (Natural History), and Cornell University.

We are indebted to Professor N. Fabritius Buchwald and Dr J. Walton Groves for helpful advice, and to Professor Sir William Wright Smith for providing the Latin description.

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(Accepted for publication 20 November 1952)

THE NOMENCLATURE OF *ARMILLARIA*, *HYPHOLOMA* AND *ENTOLOMA*

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Rigid application of the 'residue method' in the selection of generic lectotypes may lead to the interpretation of classical genera in senses quite different from those originally intended and long accepted. For *Armillaria* and *Hypholoma* the method has given results which appear to be contrary to the *International Code of Botanical Nomenclature*. We support the earlier proposals that the lectotype of *Armillaria* (Fr.) Staude be *Agaricus melleus* Vahl ex Fr., and that of *Hypholoma* (Fr.) Kummer be *Agaricus sublateritius* Fr. *Armillariella* (Karst.) Karst. and *Nematoloma* Karst. should then be relegated to synonymy under *Armillaria* and *Hypholoma*, respectively.

Adoption of the name *Rhodophyllus* Quél. (1886) is contrary to the *Code*. Those who recognize only one genus of polyhedral-spored Rhodosporeae should use the name *Entoloma* (Fr.) Kummer emend. Donk.

Mycologists who are not professional taxonomists are also affected by some recent interpretations of the International Rules of Nomenclature, which would result in undesirable changes in the names of many common species of agarics and other fungi. It is evident from the official text of the new *International Code of Botanical Nomenclature*, 1952, that some of these interpretations may now be rejected.

The difficulties arise from the selection of a lectotype for a genus which was originally erected for more than one species without designation of a holotype; if an arbitrary rule is followed it may upset the names of common or economically important species. Thus, for example, Singer & Smith (1946) rigidly followed the so-called 'residue method'; by this every genus which was split from the original assemblage of species by authors between the date of publication of the genus and the selection of a lectotype is retained and the lectotype is chosen from the species which are left. The method may sometimes be satisfactory when the splitting has been done with discretion; but with some groups of fungi, notably the Agaricales, it may happen that nothing really representative of the original conception is left under the old generic name.

Many of the arguments against the 'residue method' have been presented by Donk (1949*a, b*), who has pointed out that this method is often irreconcilable with the type method. It remained to consult the wording of the new *Code*. The rules governing the situation are two, viz.:

Article 18, of which note 3 reads: 'If no holotype has been indicated by the author who described a taxon... a substitute for it must be chosen. The author who makes this choice must be followed unless his choice is cancelled under the provisions of Art. 19.'

Article 19: 'The choice of a lectotype or neotype is cancelled if the original material is rediscovered or if it can be shown that the choice was based on a misinterpretation of the original description.'

To clarify these rules the Stockholm Congress, 1950, adopted a number of recommendations for the determination of types. Those relevant to the present problem specify that:

b. 'A *lectotype* must be chosen from among elements that were definitely studied by the author up to the time the taxon was published and included in it when it was published.'

d. 'In cases where two or more elements were included in or cited with the original description the reviewer should use his own judgment in selection of a *lectotype*, but if another author has already segregated one or two elements as other taxa the residue or part of it should be designated as the type if its essential characters correspond with the original description. If it can be shown that the element best fitting the whole published original account has been removed, it must be restored and treated as *lectotype* (Art. 19). Whenever the type material of a taxon is heterogeneous the *lectotype* should be selected so as to preserve current usage unless another element agrees better with the original description and (or) figure.' (Code, 1952, Appendix I, p. 49.)

This paragraph 'd' of the Stockholm recommendations may be regarded as the charter of the residualists, but it should be noted that the first sentence in which the residue method is approved is immediately qualified by its final clause and by the succeeding sentences.

The earliest *lectotype* selected for *Armillaria* of which we are aware is *Agaricus ramentaceus* Bull. ex Fr., chosen by Earle (1909). This choice was based on the 'First Species Rule', expressly condemned by the current rules, it being the first species in *Armillaria* as listed by Quélet when he raised the subgenus *Armillaria* Fr. to generic rank. This choice should be rejected under Articles 19 and 48. It is generally recognized that whoever raised *Armillaria* to generic rank, whether the act be accredited to Staude (1857), Kummer (1871) or Quélet (1872), was merely making a change in rank of a subgenus originally established by Fries. This is so far taken for granted that until recent years mycologists have continued attributing this and other subgenera of Fries to him in the higher rank, and have treated him as the author of combinations under these genera. The type of the genus should be one of the species in the original subgenus (Art. 48 and Rec. b quoted above). *Armillaria* originated in the *Systema mycologicum* (1821) as a 'tribus' of *Agaricus*. These subdivisions are specifically stated under Article 15 to be validly published, though Fries termed them tribes instead of subgenera. *A. ramentaceus* Bull. is not among the species included in the original publication of the subgenus *Armillaria*.

The second choice of a *lectotype* for *Armillaria* known to us is *Agaricus melleus* Vahl ex Fr., selected by Clements & Shear (1931) and supported by Donk (1949b). This was one of the original species of 1821 and is unobjectionable under Articles 18 and 19. It was rejected by Singer (1936), who was followed by Singer & Smith (1946), because Karsten (1881) had erected a genus *Armillariella*,* for which these and other authors had chosen *Agaricus melleus* as type. To retain both *Armillariella* and *Armillaria* Singer & Smith chose as *lectotype* of the latter *Agaricus luteovirens* Alb. & Schw. ex Fr. from among the residue. This species however is unacceptable for two reasons: (1) It was not in the subgenus *Armillaria* Fr. in 1821 but in the subgenus *Tricholoma*, section *genuina*!; (2) Locquin (1952),

* This was a change in rank for Karsten's subgenus (1879) for nine species of *Armillaria*.

though remarking 'Il est très regrettable que le type du genre *Armillaria* ait été ainsi choisi', nevertheless considered that the Rules required him to accept it. Study of a specimen of *Agaricus luteovirens* convinced him that *Armillaria* is now an earlier name for *Aspidella* Gilbert. *Aspidella* was founded on *Amanita vittadinii* Moretti, and Gilbert made new combinations for twenty-four species formerly placed in *Amanita*. However, Gilbert himself continued to use the latter name for these species in his *Iconographia* (1940-41), and Singer and most other mycologists now make *Aspidella* Gilb. a synonym of *Amanita*. Thus we have the ridiculous position of *Armillaria* being typified so as to make it possibly indistinguishable from *Amanita*. Singer (1951) could name only *Armillaria subcaligata* Sm. & Rea and two other doubtful species to be included with *Agaricus luteovirens* in a genus *Armillaria sensu residuo*. Locquin has now transferred to it eight species from *Amanita*. The old genus *Armillaria* as traditionally understood is worse than lost with *Agaricus luteovirens* as lectotype.

A fourth lectotype selection for *Armillaria* was that of Imai (1938), who proposed *Agaricus robustus* Alb. & Schw. ex Fr. This species, however, is commonly referred to *Tricholoma*, and its adoption as lectotype of *Armillaria* would be equally disastrous.

We believe the best solution was that of Clements & Shear in choosing as lectotype the common, cosmopolitan and distinct species *Armillaria mellea*, well known to Fries and to hundreds of plant pathologists who have never heard of the other species proposed. The recommendations of the Stockholm Congress are reconcilable with this choice. As noted above, a similar conclusion was reached before the last Congress by Donk, with whose arguments we are, in this instance, in full accord. In our view such hasty and ill-considered recombinations as those by Locquin are contrary to Article 15 of the Rules, which states that 'None may change a name without serious motives based either on more profound knowledge of facts or on the necessity of giving up a nomenclature that is contrary to the rules of this code'.

A similar situation has arisen in *Hypholoma*, where again Karsten (1879) segregated as *Nematoloma* part of the Friesian subgenus, which had been raised to the rank of genus by Kummer (1871) and Quélet (1872). The first choice of a lectotype for *Hypholoma* was *Agaricus sublateritius* Fr. by Earle (1909), on the basis of the first species rule. This was one of the species segregated in *Nematoloma* and it may have been for this reason that Clements & Shear (1931) suggested *Agaricus appendiculatus* Bull. ex Fr. as lectotype of *Hypholoma*. This was an unfortunate choice, as there has been some confusion over the interpretation of the name. In the original sense of Bulliard it is probably referable to another segregate genus, *Lachrymaria* Pat. (1887). By the residue method Singer & Smith (1946) were led to the choice of *Agaricus candolleanus* Fr. ex Fr. But it is generally recognized by modern taxonomic mycologists that this species is generically inseparable from the species of *Psathyrella* (Fr.) Quél., so that if it is upheld as lectotype of *Hypholoma* one or other of these old classical genera of Friesian origin must be lost by reduction to synonymy.

Of these three choices of lectotypes for *Hypholoma* only the first, *Agaricus sublateritius*, is to be found in the original subgenus *Hypholoma* of Fries

(1821), under the name *Agaricus lateritius* Schaeff. ex Fr. For this reason we think it should be upheld under Article 18, and the genus *Nematoloma* Karst. reduced to synonymy. We do not feel that Donk (1949*b*) was justified in rejecting *Agaricus sublateritius* in favour of *Ag. fascicularis* Huds. ex Fr. This, however, is a point of little consequence, as in any taxonomic treatment these two species are likely to remain congeneric. The epithet *sublateritius* was introduced by Fries in 1838, because in the *Systema* he had used the name *Ag. lateritius* twice, first in the subgenus *Galera* (p. 265) and again for the present species on p. 288.

The name *Entoloma* (Fr.) Kummer raises a different problem. Here there is no serious disagreement about the lectotype, for which only the closely related species *Agaricus lividus* Bull. ex Fr. and *Ag. sinuatus* Bull. ex Fr. have been proposed. Difficulties have arisen from the practice of modern taxonomists of treating as congeneric all those agarics with polyhedral spores, pink in the mass, formerly placed in *Entoloma*, *Nolanea*, *Leptonia* and *Eccilia*. For this reunited genus it has become customary of late years to revive the name *Rhodophyllus* Quél., introduced for a similar purpose in 1886.

Article 56 states that: 'When two or more groups of the same rank are united the oldest legitimate name... is retained. If the names or epithets are of the same date the author who unites the groups has the right of choosing one of them. The author who first adopts one of them, definitely treating another as a synonym or referring it to a subordinate group, must be followed.'

There is nothing in the Rules to authorize any botanist to discard all the names applied to the groups he is uniting and to replace them by a new name invented by himself. Hence, when the four genera of *Rhodosporae* are united three of them should be reduced to synonymy under the fourth. This has already been done by Donk (1949*a*), who emended the genus *Entoloma* (Fr.) Kummer to cover the same ground as *Rhodophyllus* Quél. The question whether *Rhodophyllus* is or is not a later homonym of *Rhodophyllis* Kützing (1847) does not therefore arise, but the existence of so very similar a name for a genus of red algae affords an additional argument against any attempt to conserve *Rhodophyllus* Quél. Singer's (1951, p. 611, n.) remark that 'If such a conditional conservation' (of *Rhodophyllus*) 'is legally improper this procedure should be made legal or else *Rhodophyllus* must be conserved unconditionally' may be forgotten. Such a *cri de cœur* will readily be understood by anyone who has struggled with nomenclature, but one can hardly make a serious proposal to alter the rules governing all names of Phanerogams and Cryptogams merely to save *Rhodophyllus* Quél. for the convenience of the small group of agaric specialists who have grown accustomed to its use.

It is generally agreed that there is an older generic name than any of these in the field for possible use in place of *Rhodophyllus*. This is *Acurtis* Fr., proposed in 1849 for a sterile state of *Clitopilus abortivus* (Berk. & Curt.) Sacc. Its adoption would involve such an enormous number of recombinations that there is likely to be general agreement to treat *Acurtis* as a *nomen rejiciendum*, or as the name of a form-genus in Fungi Imperfecti.

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(Accepted for publication 3 January 1953)

ONYCHOMYCOSIS CAUSED BY *SCOPULARIOPSIS BREVICAULIS*

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(With Plate 1 and 1 Text-figure)

The clinical features of onychomycosis are briefly described, and the established pathogens mentioned. The modern tendency to implicate other fungi hitherto considered saprophytic is stressed. The first case to be reported in Great Britain of onychomycosis due to *Scopulariopsis brevicaulis* (Sacc.) Bainier is described, and evidence is submitted in support of its pathogenic role in this particular case.

CLINICAL FEATURES

Onychomycosis is a chronic fungus infection of the nail plate which is fortunately rare in this country. It is most commonly found in the toe-nails and in most cases the nail involvement results from the spread of infection from another lesion. The filamentous invasion begins on the sides of the free border of the nail plate; and the fungus spreads in a fan-like fashion into the nail substance. If a drop of cedar oil is placed on the nail and viewed with a magnifying glass a delicate white network will be seen crossing the nail plate. This sign, first described by Alkiewicz (1948), is due to the formation of air channels within the keratin. These spaces are produced by the destruction of the nail substance by the invading mycelium. In the early stages of the disease a loss of lustre and yellow-green discoloration of the nail is apparent, but later the whole nail may become distorted, friable and thickened. These changes, according to Sagher (1948), are modified by the depth in the keratin at which the particular fungus elects to grow.

ETIOLOGY

In Great Britain species of *Trichophyton* may cause onychomycosis, and both Walker (1950) and Partridge (1952), working independently, found *T. rubrum* the most common. *T. interdigitale*, *T. sulphureum* and *Epidermophyton floccosum* are less frequently implicated and *Trichophyton schoenleinii* may infect the finger-nails in cases of favus of the scalp. *Candida albicans* more commonly infects the finger-nails, and is usually associated with an inflammatory bolstering of the nail-folds. Since this yeast thrives on sugary fluids, cases of this type are not uncommon in barmaids and fruit canners.

Other fungi, hitherto considered non-pathogenic, have more recently been implicated in cases of onychomycosis. Thus, Bereston & Waring (1946) and Moore & Weiss (1948) have described cases of aspergillosis of the nails, and the latter authors have cited twelve different species of *Aspergillus* which may be pathogenic. Multiple infections of the nail by

two different fungi have also been demonstrated, and Kligman (1950) has even drawn attention to a case of onychomycosis probably caused by a Basidiomycete, *Schizophyllum commune*.

Onychomycosis caused by *Scopulariopsis brevicaulis* was first described by Brumpt & Langeron (1910), who designated the organism as *S. brevicaulis* var. *hominis*, and subsequently a further thirteen French cases were recorded by Weil & Gaudin (1919). Weidman (1920) described the first American case, but although he demonstrated the fungus in the nail plate, as he more constantly cultured other fungi from the nail tissue he refused to acknowledge its pathogenicity. A more recent report of this condition was by Alkiewicz (1951), who suggested renaming the disease Acauliosis unguis from the old botanical name for this fungus: *Acaulium anomalum*.

The purpose of this paper is to report for the first time the occurrence of this disease in Great Britain, and to describe one of the author's cases in which there seemed no doubt that *Scopulariopsis brevicaulis* was the sole pathogen.

CASE REPORT

J. L. Housewife, aged 32. When first seen 18 months ago she complained of deformity and discoloration of the right large toe-nail of about 6 years duration, and more recently some erosion of the sides of other toe-nails. Examination revealed the right large toe-nail plate to be opaque and yellow. The distal half was thickened and the under surface friable and chalky. The second toe-nail showed an irregular surface with erosion of the plate at the sides. The skin of the nail-folds and inter-digital spaces was normal.

Cultures from the friable under surface of the large nail plate repeatedly grew *S. brevicaulis* in pure culture at all sites of inoculation. Intradermal tests using group extracts of other moulds have shown no reaction of acquired sensitivity.

The nail plate was removed in June 1951, and dressed with topical fungicides, but in spite of this the new nail was found to be infected when regrown.

THE PATHOGEN

Until the genus *Scopulariopsis* has been monographed it is idle to speculate as to the identity of the 'species' which have been isolated from nail tissue. Most have been near '*S. brevicaulis*', and the present isolate would appear to fall into group I of that species complex, as provisionally classified by Raper & Thom (1949), and it may therefore be designated *S. brevicaulis* (Sacc.) Bain. The characteristics of the isolate were:

In tissue

Fresh tissue mounts in 20 % potassium hydroxide show relatively few hyphae, but masses of smooth thick-walled spores amongst the nail cells (Pl. 1, fig. 2). No true chlamydospores are evident, but large ballooned hyphal elements, both terminal and intercalary in position, are to be seen. These distended cells do not have a proportionally thickened wall, and are unlike true chlamydospores in that they appear beside conidia during

active sporulation. As will be seen later, they are never seen in the submerged growth. In measurement and appearance these balloon cells are very similar to the 'chlamydospores' of Brumpt and Weidman. No *Penicillium*-like formations as illustrated by the former writer were seen on fresh tissue mounts.

Cultural characters

The mould grows well on all common mycological media incubated at 22° C., and is not restricted by variations of pH from 6.6 to 8.5. The colour varies from cream to coffee-ground and deepens with age. On Aronson's medium, however, it takes up the basic fuchsin, and forms a peach fluffy colony with a pink hue peripherally. When grown on glucose peptone agar, using either Oxoid mycological peptone or Difco bacto peptone the colony spreads broadly and is of light coffee colour. The Oxoid peptone encourages pigmentation, and the better formation of conidial tubercles. Glucose was not found to be essential for good growth, and Sabouraud's preservative medium is most suitable, especially for encouraging the conidial tuberculations. On the bile salt medium devised for culturing *Pityrosporum* (Martin-Scott, 1952) the colonies were pale grey and the conidia had a smooth elliptical outline (Text-fig. 1 d). The growth on malt agar and Czapek-Dox media was equally profuse. On the latter the colony is cream-coloured and thorny conidia are extremely rare, unless in colonies over 6 weeks old, or if trace elements, as recommended by Smith (1949), are added. Under these circumstances the colonies are coffee-coloured and the spores tuberculated and much like those grown on malt agar plates.

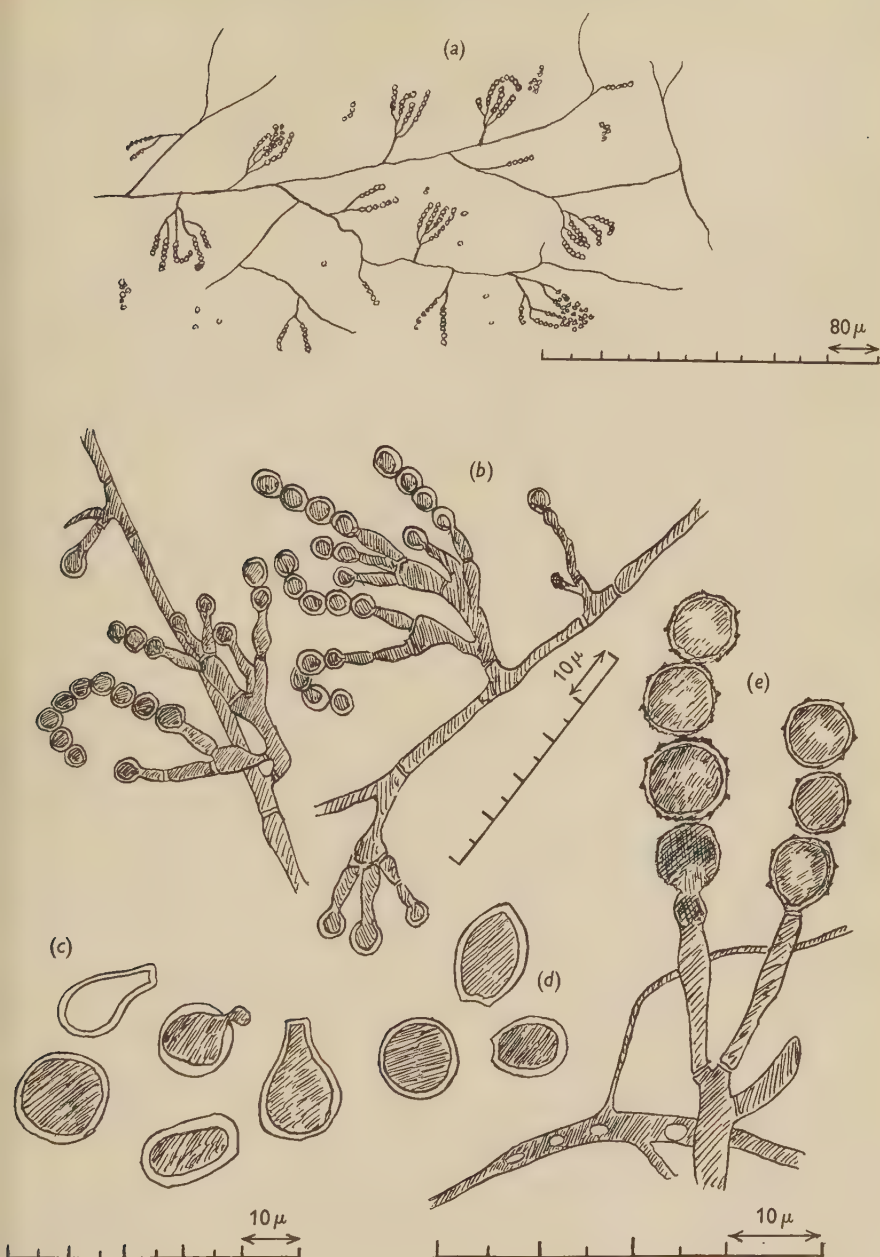
From these observations it will be appreciated that the presence or absence of tuberculations and to a lesser extent the shape of the conidia depends on the culture medium and the colony age. Furthermore, since rough-walled conidia are found in the young and old coffee-coloured colonies, and not in the cream ones, their presence probably accounts for the greater depth of colour.

On malt agar and Czapek-Dox media the colony diameter after 1 week is 3-4 cm. and is double this in a fortnight. Growth on the latter was slightly increased on the addition of trace elements. The colonies are slightly raised centrally and have a few short radial furrows. The surface is funiculose, and viewed microscopically intertwining loose hyphae are seen giving rise to short closely packed conidiophores with an aerial network of conidia.

Cultures on Czapek-Dox and malt agar media were studied daily, and details of growth on the former medium without the addition of trace elements were recorded as follows:

During the first day there was little surface growth, but a heavy mycelium appeared in the substrate and occasional racquet hyphae could be seen.

The mould gave off a slight garlic odour after 2 weeks' growth on media containing a sugar. It liquefied gelatine and digested litmus milk.



Text-fig. 1. Free-hand scale drawings of the microscopic features of the species isolated (specimens were in lacto-phenol blue). (a) General low-power view of the aerial growth seen after 6 days block culture growth on Czapek-Dox medium. (b) Magnified view from the same slide to show the irregular branching, the smooth-walled conidial formations, the young conidiophores and racquet hyphae. (c) Showing the ballooned hyphal elements which are mostly thin-walled cysts. (d) Smooth-walled and elliptical conidia after culture on my bile-salt medium. (e) The formation of tuberculate conidia on Sabouraud's preservation medium. The marked variations in hyphae are also apparent.

Microscopic characters (Text-fig. 1)

Hyphae. The segments varied between 18 and 40μ in length but were most commonly about 30μ . The usual diameter of healthy hyphae was 3μ , but variations from 1.5μ up to 4.5μ in the case of racquet hyphae were encountered.

The ballooned hyphal elements were commonly $12 \times 15\mu$, but larger ones up to $15 \times 21\mu$ could be found.

Conidiophores. In fully developed fructifications these were usually short and measured about 12μ . In young growth, when these were continuous with the sterigmata, this spore-bearing element was up to 30μ in length.

Sterigmata. These cells extending from the metula to their spore-bearing extremity had a remarkably constant length of 15μ . The diameter was 3μ but widened to 4μ peripherally immediately before final constriction at the conidium.

Conidia. The conidia were slightly longer than they were wide, typically tuberculate but often smooth.

The mean diameter varied from 4.5μ in the immature ones up to 9μ in exceptionally large ones. The average mature conidium was $6.5 \times 7\mu$. Chains of conidia commonly measured 50μ in length, but in old colonies could reach double that length.

EVIDENCE OF PATHOGENICITY

Since *Scopulariopsis brevicaulis* is an ubiquitous saprophyte and easily cultured it is not infrequently a nuisance as a contaminant. Mycologists and dermatologists have, therefore, been cautious in accepting its pathogenicity in onychomycosis, as it is not unusual to culture a mixed flora of saprophytes from normal nail tissue. The following evidence is therefore submitted to support its pathogenicity in this case:

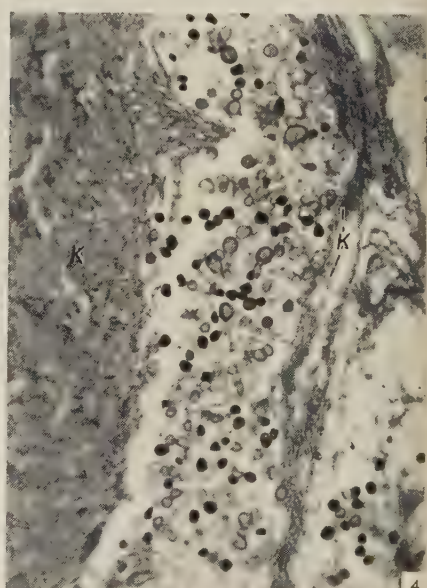
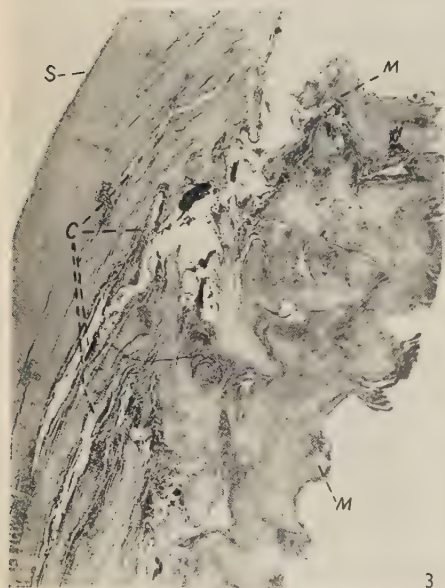
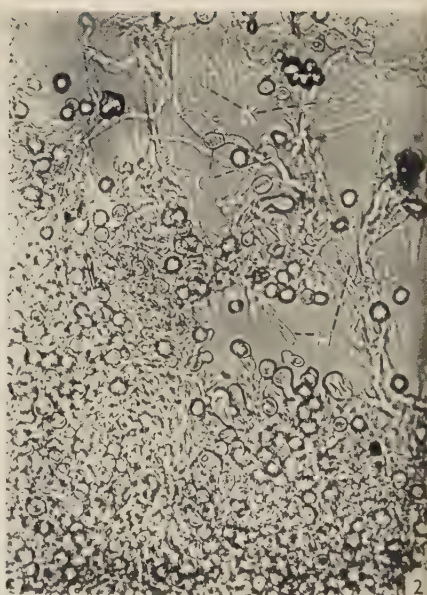
(1) The fungus has been obtained in pure culture on many occasions from different parts of the diseased nail plate, but has never been cultured from the other toe-nails of the patient.

(2) As sometimes happens after the therapeutic removal of a nail infected by an established pathogenic fungus, the new nail was also infected with the same fungus.

(3) The ability of the fungus to grow on moist keratin alone was demonstrated by sowing flakes of dry keratin from the depth of the friable nail on sterile moist filter-paper. Pure colonies of *S. brevicaulis* were produced at the sites of inoculation.

(4) The appearance of the fresh mounts suggested the spores were within the keratin and this was finally proven by cutting longitudinal sections of the nail and staining by the Gram and periodic acid Schiff methods (Pl. 1, figs. 3, 4). These showed longitudinal cleavages within the compact keratin in which germinating spores typical of *S. brevicaulis* could be identified.

(5) No other established pathogenic fungus has been cultured from the diseased nail to account for the onychomycosis, and other possible causes of nail deformity have been excluded on clinical grounds.



I wish to thank Prof. E. T. C. Spooner of the London School of Hygiene and Tropical Medicine for kindly granting the laboratory facilities, Dr Jacqueline Walker for her ever-ready co-operation, and Mr D. S. Press for the excellent photomicrographs. I am also indebted to Dr Charles Pike and his staff at the Peace Memorial Hospital, Watford, who kindly prepared the nail sections.

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EXPLANATION OF PLATE 1

- Fig. 1. Photograph of the regrowing right large toe-nail 5 months after operation. Note the irregular surface and subungual material.
- Fig. 2. Photomicrograph of nail tissue mounted in 20% potassium hydroxide. On the lower and left side the nail tissue is overgrown by thick-walled conidia, some of which are seen growing from their sterigmata (C). Septate hyphae (H) and floating keratin cells (K) are also distinguishable. Ballooned hyphal elements are seen. (× 320.)
- Fig. 3. Photomicrograph of a longitudinal section of the distal portion of the removed nail stained by Gram's method. On the left the aerial surface of the nail (S) is seen overlying the friable subungual mass (M). Clefts are seen within the keratin; and inside these darkly staining spores are just visible (C). (× 13.)
- Fig. 4. Enlarged view of fig. 3 showing an air space bounded by keratin (K) and packed with spores in various stages of germination. (× 240.)

(Accepted for publication 23 February 1953)

HYPHAL SYSTEMS AS AIDS IN IDENTIFICATION OF SPECIES AND GENERA OF THE POLYPORACEAE

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Hyphal systems of the Polyporaceae can be used as aids in generic delimitation. Species usually placed under *Fomes*, namely *F. igniarius*, *F. fomentarius*, *F. lucidus*, *F. annosus* and *F. applanatus* differ in micro-structure so profoundly that they may be considered as types of five genera, *Fomes* Kickx, *Elfvingiella* Murr., *Ganoderma* Karst., *Fomitopsis* Karst. and *Elfvingia* Karst. Genera of the Polyporus-Polystictus complex may be delimited by micro-features. Using such aids ten genera are defined, namely *Polyporus*, *Irpex*, *Coriolus*, *Lenzites*, *Coltricia*, *Inonotus*, *Hapalopilus*, *Amauroderma*, *Trametes* and *Daedalea*. *Polystictus* is held to be a synonym of *Coltricia*. Variable forms of difficult species such as '*Polyporus schweinitzii*', '*P. ochroleucus*' and '*P. occidentalis*' may be accurately identified by their micro-structure, which shows the first to be a *Coltricia*, the second a *Fomitopsis* and the third a *Coriolus*.

HYPHAL SYSTEMS

Although hyphal systems of the Polyporaceae were described and their significance defined by Corner (1932*a, b*) twenty years ago, use was not made of them in systematic studies of the family until a series of papers was published by myself (Cunningham, 1947-50). I showed them to be valuable aids in identification of species, and essential for delimiting most genera, since they enable the taxonomist to arrange related species into natural groups. This is understandable when it is realized that the morphology of a species depends upon its hyphal system; just as does a building upon its skeletal structure. In his two classical papers Corner described in detail the microscopic structure of three species, which he named *Polystictus xanthopus*, *Fomes laevigatus* and *F. senex*. I need not discuss them further, save to recapitulate certain basic features since understanding of these is essential to their application in taxonomy. Corner showed that in *Polystictus xanthopus* three series of hyphae composed the leathery fructification. These he named skeletal, binding, and generative. Skeletal hyphae provided a rigid framework, binding hyphae held the first together and formed the bulk of the tramal walls upon which the hymenium developed, generative hyphae supplied the hymenium and surface tissues. In *Fomes laevigatus* and *F. senex* he found there were two hyphal series, skeletal and generative. Corner assumed that one, two, or three hyphal systems were involved in forming the hymenophore of different species in the family. These he named respectively monomitic, dimitic and trimitic hyphal systems, admirable terms which define them precisely. His findings may be summarized as follows:

Hyphal system	Hyphal series
Monomitic	Generative hyphae only
Dimitic	Skeletal and generative hyphae
Trimitic	Skeletal, binding and generative hyphae

In 1946 I commenced detailed studies of New Zealand and Australian species of the Polyporaceae. Dissatisfied with existing methods of species delimitation, I made a detailed search of the literature to ascertain if there were other possible methods of defining these difficult plants. Among many others, Corner's papers were read carefully, and his findings appeared so promising that six months were spent in detailed studies of the 350 species then available in the herbarium. After a few weeks of experiment with different staining techniques it was found possible to identify, in transverse sections, hyphal systems of most species; or if sections were not sufficient, then to recognize them by teasing out hyphal tissues from growing margins of the plant. Results of this preliminary study were published (Cunningham, 1947*a*). They showed that three hyphal systems were involved in producing the hymenophore of different species, exactly as Corner had forecast; that not more than three were involved. Further, certain fundamental differences were noted between species with hyaline and with brown hyphae, mainly the presence or absence of clamp connexions and correspondingly of the number of nuclei in the hyphal cell. Results are summarized below.

Monomitic hyphal system: clamp connexions present in hyaline hyphae (or if absent replaced with bridging hyphae); clamp connexions absent from species with brown hyphae.

Dimitic hyphal system: clamp connexions or bridging hyphae present in species with hyaline skeletal hyphae; clamp connexions absent from species with brown skeletal hyphae.

Trimitic hyphal system: clamp connexions invariably present in generative hyphae of species with hyaline or brown skeletal and binding hyphae.

Hyphal systems and colour of the hyphae, whether hyaline or brown (when viewed under the microscope), may therefore be used as aids in generic delimitation, as will be shown.

Structure of the various hyphae forming the hymenophore may be used as aids in identification of species. Skeletal hyphae, for example, are of two general types. (1) Hyphae may be freely branched and aseptate, branches arising from a relatively short main stem. Because of their resemblance to the capillitium of species of *Bovista*, they have been termed 'bovista-type' hyphae (Cunningham, 1947*a*). Binding hyphae are also of the bovista type. (2) Skeletal hyphae may be long, thin- or thick-walled, septate or continuous, unbranched or scantily branched. They have been named 'long-type' hyphae (Cunningham, 1947*a*).

Basidial types are also useful diagnostic aids. Three types have been defined by Cunningham (1947*a*), namely 'clavate', 'merulioid', and 'honeycomb'. The clavate type is common to most species; the merulioid type is present in most species of *Merulius* and many polypores possessing hyaline hyphae and small allantoid spores; the honeycomb type is confined to species with setae embedded in the hymenial layer. Such inclusions as setae, cystidia or conducting vessels are constant for each species and therefore serve as useful aids in specific diagnosis.

USE OF HYPHAL SYSTEMS IN GENERIC DELIMITATION

Taxonomists who have worked critically over the polypores of a region realize that it is not possible to identify species from descriptions published by early workers. Even with specimens for comparison it is difficult and often impossible to make correct identifications by aid of macro-features commonly used as specific characters, namely shape, size and colour of the hymenophore, whether stipitate, sessile or resupinate, colour and texture of the context. Such features may be adequate for well-known temperate species but break down when applied to tropical or subtropical forms, which change appreciably and often profoundly under more luxuriant growth conditions. This may be illustrated by reference to Australasian collections of polypores in Kew herbarium. The collections were examined critically by myself in 1948 and 1951, and results published in two papers (Cunningham, 1949*a*, 1950*b*). In 1948 there were 829 collections from Australia and New Zealand in the herbarium, representing 274 valid species; 389 were incorrectly named or referred to species not present in the region; and no less than 220 synonyms were erected on specimens of valid species. (Changes of generic names have been ignored in this computation since as yet there is no stability in generic nomenclature of the family.) In the course of this comprehensive study it was found possible to identify with certainty, by use of hyphal systems and other microfeatures, all but a dozen of the collections at Kew, even though so many were represented by single specimens, often poorly preserved or fragmentary.

Let us now discuss briefly the use of hyphal systems for delimiting genera of the Polyporaceae. From 9 to 186 genera have been recognized by different workers, most employing for generic characters the macrofeatures previously mentioned. More recently a few workers have used as generic features colour and markings of spores, whether they are amyloid or not, presence of setae or cystidia, etc. Stability in generic nomenclature cannot be achieved by use of such features alone, as is evident by the present confused state of polypore classification. Consequently other diagnostic aids must be sought which are to be found, I believe, in hyphal systems and other microfeatures.

Consider the genus *Fomes*, used in its broad sense to include perennial species with round pores arranged in strata. Kickx (1867) was the first to employ the name for a genus, and under it placed *F. salicinus*, *F. igniarius*, *F. fomentarius* and *F. lucidus*. Three possess brown, one hyaline hyphae; two possess trimitic hyphal systems with clamp connexions; two dimitic hyphal systems without clamp connexions. This diversity clearly indicates that the species represent several genera, one of which must be the type species of *Fomes*. *F. lucidus* possesses hyaline hyphae, a trimitic hyphal system and peculiar spores with a double wall, the inner provided with coarse spines extending into the outer wall giving to it an echinulate appearance. Spores of this type will be referred to as ganodermous. The species was by Karsten (1881) chosen as the type of *Ganoderma*, obviously a valid genus in view of this evidence. *Fomes igniarius* and *F. salicinus* possess brown hyphae and dimitic hyphal systems without clamp connexions. They are obviously

co-generic; and as *F. salicinus* has not been proposed as a type species it need not be further considered. *F. fomentarius* possesses brown hyphae and a trimitic hyphal system with clamp connexions in the generative hyphae. It is therefore not co-generic with *F. igniarius*. There are upwards of 150 species of *Fomes* with brown hyphae and dimitic hyphal systems, as in *F. igniarius*, and only about eight possessing brown hyphae and trimitic hyphal systems, as in *F. fomentarius*. Consequently, stability in nomenclature would be best secured if the type species for *Fomes* were regarded as *F. igniarius*. A generic name for *F. fomentarius* and related species lies to hand in *Elfvingiella* which Murrill (1914) erected with *E. fomentaria* as type.

Two additional species usually placed under *Fomes* now require consideration, namely *F. annosus* and *F. applanatus*. Both possess dimitic hyphal systems without clamp connexions in the generative hyphae. They are not co-generic, however, since the skeletal hyphae of *F. annosus* are hyaline and unbranched and spores are smooth and hyaline; whereas in *F. applanatus* skeletal hyphae are brown, freely branched, and spores are ganodermous. Neither resembles the type species of *Fomes*, *Ganoderma*, or *Elfvingiella*, so both must be considered under other generic names. Karsten (1881, 1889) had provided these in *Fomitopsis* with *Fomes annosus* as type species, and *Elfvingia* with *Fomes applanatus* as type. *Ganoderma* cannot be employed as a generic name for the latter species, since the type species is *Fomes lucidus* (the only species listed by Karsten), a markedly distinct plant, as has been shown.

Thus the old genus *Fomes* may be divided into five well-defined genera which can be defined with certainty by the following main characters:

Hyphal system dimitic, without clamp connexions.

Hyphae hyaline, spores smooth.

Hyphae brown, spores smooth.

Hyphae brown, spores ganodermous.

Hyphal system trimitic, generative hyphae with clamp connexions.

Hyphae hyaline, spores ganodermous.

Hyphae brown, spores smooth.

Fomitopsis (*F. annosa*)

Fomes (*F. igniarius*)

Elfvingia (*E. applanata*)

Ganoderma (*G. lucidum*)

Elfvingiella (*E. fomentaria*)

Other genera also may be delimited by aid of hyphal systems. Consider those used but not clearly defined by Fries, namely *Polystictus*, *Polyporus*, *Trametes*, *Lenzites* and *Daedalea*.

Polystictus, in the broad sense in which it has been employed by most taxonomists, embraces species of several genera with hyaline and coloured hyphae, monomitic, dimitic and trimitic hyphal systems. Fries (1851) erected the genus to contain nine sections, of which the first 'Stirps *Polystictus perennis*' was composed of *P. parvulus*, *P. connatus*, *P. bulbipes* and *P. concinnus*. *P. parvulus*, *P. bulbipes* (a synonym of *P. oblectans*) and *P. connatus* (a synonym of *P. perennis*) closely resemble one another in micro-structure, possessing long ribbon-like brown hyphae, a monomitic hyphal system without clamp connexions, and basidia of clavate type. It is evident, therefore, that his concept of this first stirp was of a group of species resembling *P. perennis*. Thirty years previously Gray (1821) erected *Coltricia* to contain one of the species (*C. connata* = *Polystictus perennis*) later placed by Fries under his first stirp of *Polystictus*. *Coltricia* is therefore

a valid genus with *C. perennis* as type; and *Polystictus* is either a synonym or, if conserved, a name to be applied to the 'type' of some other stirp of this heterogenous genus.

Polyporus, like *Polystictus*, is by most taxonomists used for species of several genera possessing hyaline and brown hyphae, monomitic, dimitic, and trimitic hyphal systems. Various workers have attempted to subdivide *Polyporus* on macrofeatures, but with indifferent success as is shown by the confused state of the literature. By the aid of hyphal systems it is possible to bring together related species. Thus those with hyaline hyphae and trimitic hyphal systems form a natural group to which Quélet (1886) gave the name of *Coriolus* with *C. zonatus* as type species. Species with hyaline hyphae and monomitic or dimitic hyphal systems may be treated under *Polyporus*, or further subdivided into species with monomitic and dimitic systems. Such a division may be made ultimately, but I have treated both under *Polyporus* because of practical difficulties encountered in interpreting species with sclerotoid context.

Species with brown hyphae, usually placed under *Polyporus*, *Polystictus* and *Trametes*, may be segregated similarly. *Coltricia* has been discussed. Species with a monomitic hyphal system, honeycomb basidial type and setae in the hymenium form a small natural group for which Karsten (1879) proposed the genus *Inonotus* with *I. cuticularis* as type species. Those with dimitic hyphal systems, without clamp connexions, may be placed under *Hapalopilus* Karst. and *Amauroderma* Murr., the former with smooth, the latter ganodermous spores.

Trametes, from its introduction (1836), was not clearly defined. Fries did not indicate a type species nor any constant feature by which it could be separated from the *Polyporus* complex; consequently *Trametes* has become a depositary for diverse species of several genera. If the type species be taken as *Trametes odorata*, then it is possible to define the genus concisely and bring together related species. Characters of *T. odorata*, which then become the generic characters of *Trametes*, are brown hyphae, trimitic hyphal system with clamp connexions in generative hyphae, clavate basidial type, and smooth spores. *Trametes* becomes then, in fact, the brown hyphal complement of *Coriolus*.

Daedalea and *Lenzites* also offer difficulties if segregated upon differential features used by taxonomists, namely the labyrinthiform or lamellar hymenial surface. Under subtropical conditions such features change to a surprising degree; for in our herbarium are collections of *Daedalea trabea* and *Lenzites betulina* with poroid, lamelloid, daedaloid or irpicoid hymenia. Sometimes all or several conditions may be present in the same collection, or even in one specimen. If the type species are taken to be *Daedalea confragosa* and *Lenzites betulina* respectively, it becomes an easy matter to define these two genera. Both possess trimitic hyphal systems with clamp connexions in the generative hyphae; *Lenzites betulina* has hyaline hyphae, *Daedalea confragosa* brown. Consequently separation may be made upon this one easily seen feature irrespective of hymenial form.

The *Polyporus*-*Polystictus* group, in its widest sense, may be subdivided by the aid of hyphal systems and related micro-features on the following lines:

- Hyphae hyaline; basidial types clavate or meruloid; with clamp connexions or bridging hyphae in the generative hyphae.
- Hyphal system monomitic or dimitic.
- Pores round or oval. **Polyporus** (*P. arcularius*)
- Pores becoming irpiciform with a permanent poroid border. **Irpex** (*I. lacteus*)
- Hyphal system trimitic.
- Pores round or oval. **Coriolus** (*C. zonatus*)
- Pores lamellar or labyrinthiform. **Lenzites** (*L. betulina*)
- Hyphae brown: basidial type clavate or honeycomb.
- Hyphal system monomitic, without clamp connexions.
- Basidial type clavate; setae absent. **Coltricia** (*C. perennis*)
- Basidial type honeycomb; setae present. **Inonotus** (*I. cuticularis*)
- Hyphal system dimitic, without clamp connexions.
- Spores smooth. **Hapalopilus** (*H. lutescens*?)
- Spores ganodermous. **Amauroderma** (*A. schomburgkii*)
- Hyphal system trimitic, with clamp connexions.
- Hymenophore with round pores. **Trametes** (*T. odorata*)
- Hymenophore labyrinthiform or lamellar. **Daedalea** (*D. confragosa*)

Let us now discuss briefly the use of hyphal systems in placing difficult species under their related genera. *Polyporus schweinitzii* has proved a problem to many taxonomists since in different floras it has been treated as a *Polyporus*, *Polystictus*, *Fomes*, *Daedalea*, *Phaeolus*, *Cladomeris*, or *Inodermus*. Possessing the same micro-structure as species of *Coltricia* it is obviously a member of that genus. *Polyporus ochroleucus* assumes so many diverse forms that it has been named as new about twenty times, and placed under *Polyporus*, *Polystictus*, *Fomes*, *Trametes* and *Ungulina*. The hyphal system shows it to be a *Fomitopsis* with such a distinctive micro-structure that specimens may be identified readily irrespective of form. *Polyporus occidentalis*, a common subtropical and tropical species, assumes so many diverse shapes and hymenial forms that it has been placed under *Polyporus*, *Polystictus*, *Trametes*, *Daedalea* and *Irpex*, and is burdened with at least a dozen synonyms. The hyphal system is that of *Coriolus*, related to *C. hirsutus*. Our common *Daedalea trabea* may assume poroid, daedaloid, lamelloid or irpicoid hymenial forms, grow pileate or resupinate, range in colour from orange, through grey, ferruginous, to umber. Most of these conditions have been named as distinct species; yet sections show that all are forms of one species since the micro-structure is identical in each variant.

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(Accepted for publication 3 March 1953)

FUNCTION OF THE MYCELIAL STRANDS IN SUBSTRATE COLONIZATION BY THE CULTIVATED MUSHROOM, *PSALLIOTA HORTENSIS*

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(With Plate 2)

Experiments are described showing that for successful colonization of a suitable prepared compost by mycelial strands of the cultivated mushroom fungus, a certain inoculum potential is necessary; if inoculum potential is only just adequate, colonization is greatly delayed. Inoculum potential at the growing tips of the mycelial strands appears to vary directly with size and vigour of the inoculum food-base, and inversely with distance from this food-base. New mycelial strands soon grow out from freshly colonized compost into new soil, but not into soil already occupied by older strands.

INTRODUCTION

Mycelial strands are the channels through which nutrients are translocated from a colonized substrate to another potential substrate, which may lie some distance away in the soil from the first. This is merely a statement of the observed facts, further consideration of which suggests several problems for investigation. In the mushroom fungus, the mycelial strands appear to be formed by the growing together of individual hyphae; although a strand may continue to increase in thickness through the accretion of further individual hyphae from the substrate at its base, yet it remains a simple and undifferentiated aggregation of hyphae. It thus seems unlikely that translocation of nutrients along such a simple mycelial strand is any more rapid than it is along one of the individual hyphae composing such a strand. What, if any, is therefore the advantage to such a lignin-decomposing saprophyte of mycelial aggregation into strands? It has been suggested that such aggregation affords some protection against desiccation; apart, however, from the fact that desiccation is not an important natural hazard for fungi in most soils, there is evidence from experiments with various root-infecting fungi that mycelial strands afford little extra protection against drying-out.

A clue to this problem, as to so many others, has been found in the work of Buller (1931, ch. 4), to which attention has recently been re-directed (Garrett, 1951). In experiments with *Coprinus sterquilinus*, Buller showed that freshly dropped dung balls of the horse could be rolled in the spores of this fungus until they were blackened, and yet no fruit bodies of *C. sterquilinus* developed upon the inoculated dung balls, indicating that effective colonization had failed to occur. Buller attributed this failure to the fact that the dung balls were already colonized at the time of evacuation by germinating spores of other coprophilous species that had been devoured by the animal along with the herbage on which it fed. Buller

then showed in a further experiment that if dung balls were inoculated with a vigorous mycelial culture of *C. sterquilinus* on sterilized horse dung, effective colonization of the dung balls followed, and the fungus produced its fruit bodies thereon. These observations by Buller suggest that a certain *inoculum potential* may be necessary for colonization of such a substrate. Mycelial strands are the obvious means whereby nutrients are translocated from the old substrate—the *food-base*—to the new one to be colonized, in the necessary concentration to provide an adequate inoculum potential. Such an inoculum potential is built-up by a pooling of all the nutrients at the disposal of each of the individual hyphae composing the strand, resulting in a concentration at the point of contact with the new substrate.

The need for an adequate inoculum potential for infection of living host roots has been established by experiments with various root-infecting fungi, and is presumably necessary in order to overcome host resistance (Garrett, 1944, p. 26). The experiments of Buller, cited above, appear to be the first demonstration of the need for a certain inoculum potential in saprophytic colonization; a similar effect was later observed by Blair (1943) with *Corticium solani*, which grows as a saprophyte through unsterilized soil if the initial inoculum potential is adequate. In considering the reasons for which a certain inoculum potential may be necessary for colonization of a lignin substrate by *Psalliota* spp., it is necessary first to remember that lignin decomposers are normally the last members of the fungal succession to develop on decomposing plant remains, and that they develop upon a substrate from which the simpler and more readily utilized carbon compounds have been removed by the earlier colonizers, and are hence not available, except perhaps in very small amounts, to the lignin decomposer. It is possible that the earlier colonizers, though much diminished in activity owing to the exhaustion of their own substrate, may yet exert some antagonistic effect on colonization by the lignin decomposer, if only through the excretion of carbon dioxide for instance. Brown (1922) showed that the retarding effect of carbon dioxide upon spore germination and mycelial growth of various moulds was greatest when the energy of growth was least, i.e. on a poor substrate, and it is thus possible that the necessity for a certain inoculum potential may be imposed upon the lignin decomposer by the occurrence of such antagonistic effects. It is also likely, however, that an appreciable expenditure of energy is necessary for lignin decomposition, and that this chiefly determines the level of inoculum potential necessary for its initiation. This second possibility finds some support from the experiments of Gottlieb, Day & Pelczar (1950) on the growth of *Poria subacida*, *Polyporus abietinus* and *Polystictus versicolor* on native lignin isolated from red spruce wood. When both 0.01 % glucose and 0.5 % lignin were provided together as carbon sources, the growth with all three fungi was considerably greater than the sum of the growths made on 0.01 % glucose and 0.5 % lignin separately. Although Gottlieb *et al.* have preferred to suggest that lignin facilitated utilization of the glucose, it is equally possible that glucose facilitated utilization of the lignin. It seems doubtful, indeed, whether more efficient utilization of so low a concentration of glucose as 0.01 % could have produced a growth

response as large as that shown, whereas more efficient utilization of 0.5 % lignin might well have done so.

The experiments described below have been designed to investigate the effect of inoculum potential upon compost colonization by the mushroom fungus.

EXPERIMENT ON NUTRIENT STATUS OF THE INOCULUM

The mushroom fungus has been found to grow better upon malt-extract agar than upon any of the other common media tested, and for the purpose of this experiment, colonies were grown upon malt-extract agar of the following concentrations: 0.5, 1, 2, 4 and 6 % malt extract. Inoculum disks were taken with a 15 mm. cork borer from colonies 17 days old at 25° C.; the depth of agar was 3 mm. (20 ml. per 9 cm. plate). Two kinds of inoculum disk were taken from each type of agar: 'marginal' disks cut so that the outer edge of the disk just touched the mycelial margin of the colony; 'submarginal' disks taken immediately inside the ring of marginal disks from each colony. In a study of mycelial strand production by similar agar disks of *Helicobasidium purpureum*, Garrett (1946) found that stronger and more consistent strand production was obtained from submarginal disks, which was attributed to the higher nutrient status of the older mycelium in such disks. The inoculum disks were placed, mycelial face upwards, at the bottom of glass specimen tubes of length 7.5 cm. and diameter 1.7 cm.; for each of the five types of agar, six tubes received marginal disks and six received submarginal disks, making sixty tubes in all. To each tube was then added 4 g. of a synthetic wheat straw compost suitable for mushroom cultivation, supplied by the Mushroom Research Station at Yaxley, Peterborough (Edwards, 1950). Upon arrival, this compost was incubated in plugged bottles for 48 hr. at 55° C., to simulate the final 'peak heating' that compost normally undergoes after the beds have been filled; thereafter, it was stored for 3 weeks at laboratory temperature before use in this experiment. After addition of the compost, tubes were plugged with cotton-wool, and incubated at 25° C. The progress of macroscopically visible compost colonization was recorded at approximately weekly intervals from 17 to 49 days, but only the first and last observations are given in Table 1.

In comparing the first and final sets of observations, it will be seen that in some tubes in which no sign of colonization could be seen at 17 days, complete colonization of the compost had occurred after 49 days. Two criteria of compost colonization were available: (1) progressive development of the white mycelial strands of the mushroom fungus; (2) a characteristic colour change from the dark brown of uncolonized compost to the light brick-red colour of compost colonized by the mushroom fungus. In any tube showing these unmistakable signs of progressive but as yet incomplete colonization at one weekly observation, colonization was invariably complete after another week at 25° C.

The results of this experiment show, first, that colonization of the compost failed to occur if inoculum potential was too low and, secondly, that if inoculum potential was barely sufficient, colonization was delayed. Thus with inocula of 4 and 6 % malt, compost colonization was rapid,

and appeared complete in all 12 tubes of each series even before the first recording at 17 days. With 0.5 % malt inoculum, on the other hand, only 1/12 tubes showed colonization after 49 days; colonization in this tube was already well advanced after 17 days, and must be attributed to a chance coincidence of favourable circumstances. With 1 % malt inoculum, colonization was delayed, increasing from no visible colonization at

Table 1. *Colonization of compost by the mushroom fungus from agar inocula of different malt-extract concentration*

Tube nos. ...	Marginal disks						Submarginal disks					
	1	2	3	4	5	6	1	2	3	4	5	6
After 17 days												
0.5 % malt	+	—	—	—	—	—	—	—	—	—	—	—
1 % malt	—	—	—	—	—	—	—	—	—	—	—	—
2 % malt	+	+	+	—	—	—	+	+	+	+	—	—
4 % malt	+	+	+	+	+	+	+	+	+	+	+	+
6 % malt	+	+	+	+	+	+	+	+	+	+	+	+
After 49 days												
0.5 % malt	+	—	—	—	—	—	—	—	—	—	—	—
1 % malt	+	—	—	—	—	—	+	+	+	—	—	—
2 % malt	+	+	+	+	+	+	+	+	+	+	+	—

+ = colonization, complete; +* = colonization, not yet complete; — = no colonization.

17 days to colonization in 4/12 tubes after 49 days. Similarly, visible colonization in the 2 % malt inoculum series increased from 7/12 tubes (incomplete in one) after 17 days to 11/12 tubes after 49 days. The superiority of submarginal over marginal inoculum disks can be seen in the final results with 1 % malt inoculum (colonization in 3/6 tubes as against 1/6 tubes). Although a similar superiority is no longer apparent in the 2 % malt inoculum series after 49 days, yet colonization was more rapid with submarginal disks, visible colonization having occurred after 24 days in 5/6 tubes (incomplete in one) with submarginal disks, but in only 3/6 tubes with marginal disks.

EXPERIMENT ON POSITION AND DURATION OF THE INOCULUM

This experiment was carried out in glass tubes of internal diameter 1.9 cm. and length 25 or 38 cm.; the soil employed was a light loam from a Cambridge garden. The bottom of each tube was plugged with cotton-wool, and a 3 cm. column of air-dry soil was added, and then moistened to 60 % saturation (saturation capacity 45 ml. water per 100 g. air-dry soil). This was followed by 1 g. of a commercial pure culture mushroom spawn (in air-dry condition, as marketed), occupying 2.25–2.5 cm. length of tube. A preliminary experiment had shown that this batch of spawn produced a strong growth of mycelial strands, and that strand growth started earlier if the spawn was allowed to take up water gradually from the moist soil, rather than directly from a pipette. Further sections of air-dry soil were then added, and brought up to 60 % saturation by addition of water from a graduated pipette. Soil columns of four different lengths were set up above the spawn inoculum: 3, 6 and 12 cm. (in 25 cm. tubes)

and 18 cm. (in 38 cm. tubes). Sixteen replicate tubes were set up for each length of soil column. Finally, 5 g. moist Yaxley wheat straw compost was added above the soil column in each tube and pressed down; the compost was from the same stock as that employed in the first experiment, but was used immediately after 48 hr. peak heating at 55° C., without any intervening period of storage. Finally, the top of each tube was plugged with cotton-wool, and the 64 tubes were incubated at 25° C.

Growth of mycelial strands from the spawn inoculum started evenly and promptly in all tubes, taking 9–12 days to grow through 3 cm. soil, 14–18 days for 6 cm., 22–27 days for 12 cm., and 34–38 days for 18 cm. soil; in one 18 cm. soil column tube, strand growth was poor and failed to reach the compost, so the tube was discarded. All tubes in which the mycelial strands were nearing the compost were inspected morning and evening; as soon as the advancing margin of mycelial strands reached the compost in any tube, the spawn inoculum was removed, and a similar tube showing a comparable extent of strand growth was set aside to serve as an untouched control. For each soil column length series, therefore, the inoculum was removed from 8 tubes (only 7 tubes available in the 18 cm. series), and left untouched in 8 control tubes.

The results of this experiment showed clearly that removal of the inoculum at time of contact between mycelial strands and compost delayed compost colonization by the mushroom mycelium. This delay was shown both in development of mycelial strands through the compost and in development of the characteristic colour change of the compost from dark brown to light brick-red. The development of mycelial strands never became so heavy in the tubes from which the inoculum had been removed as in the control tubes; nevertheless, as judged by colour change and strand development, colonization of the compost was eventually complete, in spite of inoculum removal, in 7/8 tubes with 3 cm. soil, in 8/8 tubes with 6 cm., in 7/8 tubes with 12 cm., and in 5/7 tubes with 18 cm. soil. In all control tubes, rapid and complete compost colonization occurred.

The delay in compost colonization occasioned by removal of the inoculum food base increased with increase in length of the intervening soil column, and is illustrated in Pl. 2, showing effect of inoculum removal in the 6 and 18 cm. soil tubes, photographed 18–21 and 18–22 days, respectively, after inoculum removal. On the assumption that the level of inoculum potential in the growing tips of the mycelial strands declines with increasing distance from the inoculum food-base, it is reasonable to suppose that severance of connexion with the food-base would produce the greatest effect on compost colonization at 18 cm. distance, at which inoculum potential would most nearly approach a critically low level for colonization.

Pl. 2 also shows another feature of interest in the 18 cm. soil columns. In preparation for the photograph each tube was turned so as to show the maximum strand development in the soil columns. Whereas in the control tubes, the mycelial strands are coarse and persistent, in the tubes from which the inoculum has been removed, the strands have either vanished or are disintegrating. After a further 9 days (27–31 days after inoculum

removal), the original mycelial strands had completely disappeared from all 7 tubes without the original inoculum, but had persisted in the 8 control tubes. In the 5 inoculum-removed tubes in which compost colonization had occurred, a growth of new strands had been put out in the reverse direction, i.e. back from the colonized compost, for distances of 4.5–11 cm. No such growth of new strands had occurred in any of the control tubes, and it seems that such growth must have been inhibited by the persistence of the original strands from the inoculum. If the growth of fresh strands from the colonized compost had depended solely upon the degree of colonization, it should have occurred earlier in the control than in the inoculum-removed tubes. This supposition was then tested by addition of a new 3 cm. soil column above the compost to the control tubes; strands grew out into this fresh soil within a few days in all the tubes, but still no strands were put out into the soil columns below the compost, in which the original strands still persisted. This observation recalls one by King, Loomis & Hope (1931) on the growth of *Phymatrichum omnivorum* from a food-base of infected cotton roots through glass tubes of sterilized sand; they found that if a pre-existing growth of mycelial strands was broken up by vigorous shaking of the tubes, a fresh growth of strands was made from suitable inoculum.

In conclusion, some indication must now be given of the degree of significance that can be attached to the results of the experiment just described, which was only one of a number of similar experiments actually carried out. The precise effect of removing the inoculum food-base in different experiments has appeared to depend upon the inoculum potential of the growing tips of the mycelial strands at the time they reach the compost. If the inoculum is too small, insufficiently vigorous or too far away, removal at time of contact between strands and compost may prevent colonization altogether; if, on the other hand, the inoculum is vigorous and at an optimum distance from the compost, then the effect of removal on colonization may be comparatively slight. The resistance to colonization of the compost, and especially the microbiological resistance, must also vary somewhat from one experiment to another, and even within the same experiment, inasmuch as the strands reach the compost at different times after growth through soil columns of different lengths, though such a possible effect is not deemed of sufficient importance to invalidate the conclusions reached above. If compost is inoculated with mushroom spawn before it has been properly 'made', i.e. before microbiological decomposition of the simpler carbon compounds is complete, the spawn fails to run, however vigorous the inoculum; the chemical changes involved in composting for mushroom cultivation have been elucidated, especially by Waksman and his associates (for references, see Garrett, 1951).

The general conclusion that can be drawn from this investigation, therefore, is that success in compost colonization by the mushroom fungus, and the time taken to achieve it, depends upon the inoculum potential of the growing tips of the mycelial strands, and that this in turn depends both upon the vigour of the inoculum and upon its distance from the compost.

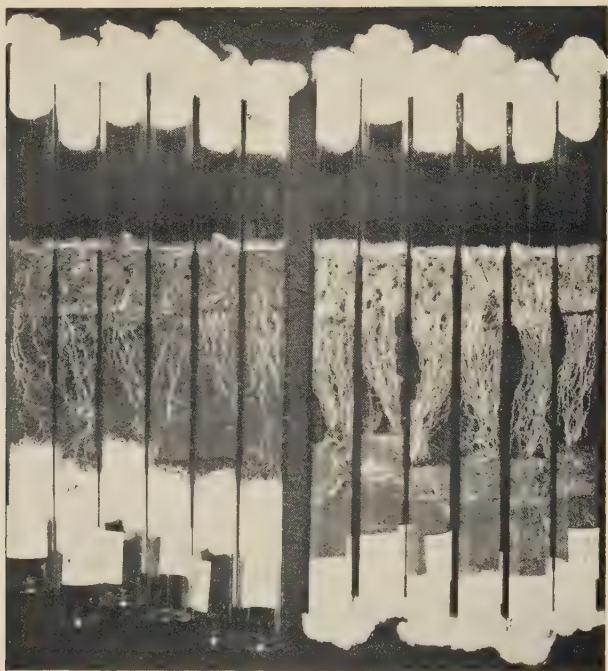


Fig. 1.

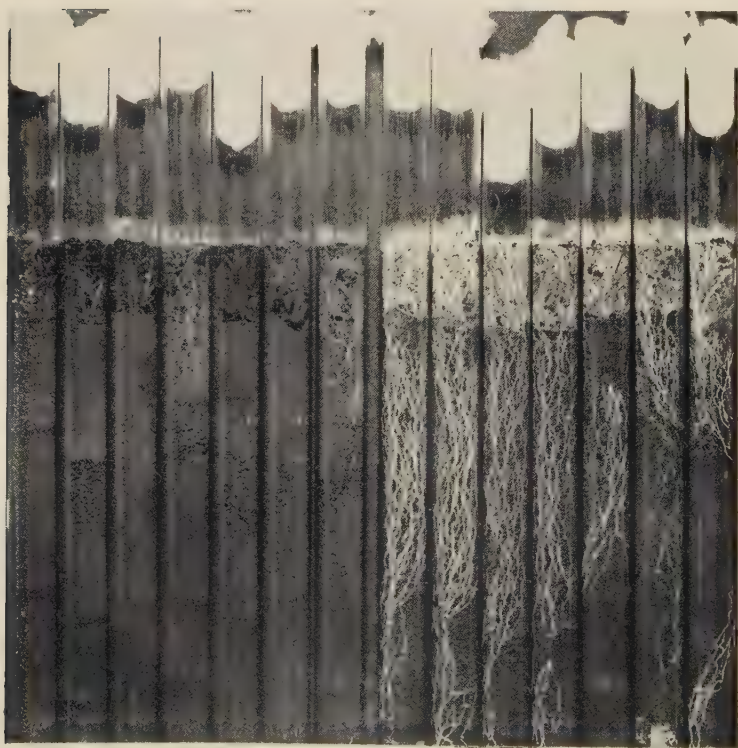


Fig. 2.

I am especially indebted to Dr R. L. Edwards, Director of the Mushroom Research Station at Yaxley, Peterborough, for advice concerning mushroom cultivation, and also for the sample of synthetic compost used in these experiments.

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EXPLANATION OF PLATE 2

- Fig. 1. On left, 6 tubes in which inoculum food-base at 6 cm. distance from layer of compost at top of tube had been removed just as mycelial strands reached the compost, 18-21 days before photograph. On right, 6 control tubes in which the inoculum food-base was left undisturbed.
- Fig. 2. Similar to Fig. 1, but compost at 18 cm. distance from inoculum food-base; tubes photographed 18-22 days after mycelial strands reached compost. Note that inoculum removal from 7 tubes on the left has caused a greater delay in compost colonization than that shown in Fig. 1. Note also the disintegration of strands following inoculum removal.

(Accepted for publication 9 March 1953)

PYRENOPEZIZA THALICTRI (PECK) SACC. IN BRITAIN

By W. D. GRADDON

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(With 6 Text-figures)

Pyrenopeziza thalictri (Peck) Sacc. is described from the type collection and is recorded from Yorkshire. *P. osiliensis* Vestergren is considered to be the same fungus.

In 1950 Mr W. G. Bramley kindly sent me, from Yorkshire, superb material of an unnamed *Pyrenopeziza* on dead stems of *Thalictrum flavum* L. The characters of the fungus agreed well with those given for *Peziza thalictri* Peck on *Thalictrum* stems in New York State and for *Pyrenopeziza osiliensis* Vestergren on plants of the same genus on Osil Island in the Baltic.

Study of microtome sections of authentic material has convinced me that these two collections and that from Yorkshire show no greater differences than should be expected within a single species growing on different host plants and ranging as widely as from North America through Britain and Germany to the Baltic Sea. In my opinion, the European collections should be regarded as examples of Peck's fungus.

As the study of type material has been involved, it seems desirable to publish full details of the plants examined. The following description of the species is drawn from Peck's type material in the herbarium of the New York State Museum at Albany.

***Pyrenopeziza thalictri* (Peck) Sacc., *Syll. Fung.* **8**, 360 (1889)**

syn: *Peziza thalictri* Peck, *Ann. Rep. N.Y. St. Mus.* **29**, 55 (1878).

Pyrenopeziza osiliensis Vestergren, *Bot. Notiser*, p. 40 (1900).

Beloniella osiliensis (Vestgr.) Rehm, *Ber. bayer. bot. Ges.* **13**, 181 (1912).

Dry *apothecia* closely gregarious in large colonies; visibly erumpent through the host epidermis which is split longitudinally and not much up-lifted. About 400μ across (550μ after soaking), rather deeply cupulate, with incurved margin which hides the hymenium; externally brownish black and scabrous, paler towards the margin which is subhyaline and fimbriate. Attached to the host by a central base, $80-120\mu$ across, composed of somewhat vertically aligned hyaline or brownish cells, $5-8\mu$, which merge into the overlying hypothecium. Several layers of host cells beneath this base are filled with brown hyphae. Lower excipulum $25-35\mu$ thick, of one to three outer layers of brown cells, $5-7\mu$ across, with dark walls and two to three inner layers of hyaline cells, $8-12\mu$ across, with hyaline walls. Upper excipulum $15-20\mu$ thick, of two to three layers

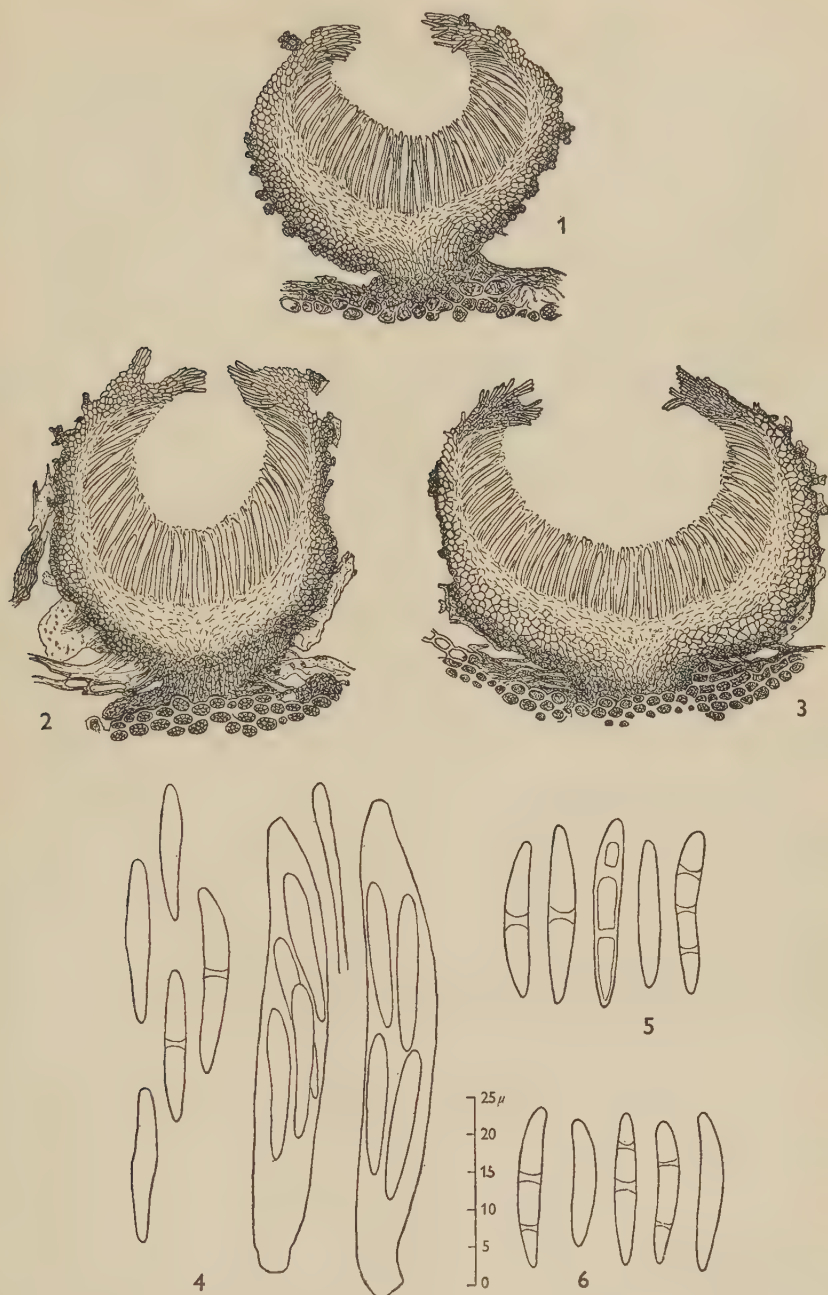


Fig. 1. Median section of apothecium from the type collection of *Peziza thalictri* Peck. $\times 125$.
 Fig. 2. Median section of apothecium from Yorkshire material. $\times 125$.
 Fig. 3. Median section of apothecium from Vestergren, Micromyc. rar. select. no. 226. $\times 125$.
 Fig. 4. Hymenium components of *Peziza thalictri* Peck.
 Fig. 5. Spores of Vestergren, Micromyc. rar. select. no. 226.
 Fig. 6. Spores from the Yorkshire material.

of hyaline cells. Margin of elongate, hyaline, septate hyphae, $25-40 \times 2.5-4 \mu$, considerably overhanging the hymenium. The cortex gives rise, here and there, to projecting clusters of dark brown cells which give the apothecium its scabrous appearance. Hypothecium hyaline, $15-20 \mu$ thick. *Asci* $60-70 \times 8-9 \mu$, rather broadly cylindric-clavate, containing no more than four developed spores; pedicel short; apex rather pointed, the pore strongly blue in Melzer reagent. *Spores* $(18-21-26-(29) \times 2.5-3.5 \mu$, hyaline, clavate, mostly continuous but some with indications of a median septum. *Paraphyses* very slender, very slightly enlarged above to $2-2.5 \mu$. (Figs. 1, 4).

Habitat: Base of dead stems of *Thalictrum cornuti*, Center, N.Y. State. May.

PYRENOPEZIZA OSILIENSIS Vestergren in Herb. Kew, as *Micromyc. rar. select. no. 226*, on *Thalictrum* stems, Osil Island, June 1899. In this exsiccatum the dry apothecia are up to 550μ across and each one is within a little 'tent' of uplifted host epidermis; it would appear that with these particular *Thalictrum* stems the epidermis is more readily detached than is the case with stems bearing the American and British apothecia. The excipular cells are a little larger than in the type material. The spores are $20-25 \times 3-4 \mu$, and the spore content is often broken up to give an appearance of incipient 1-, 2- or 3-septation. (Figs. 3, 5).

PYRENOPEZIZA THALICTRI (Peck) Sacc., Herb. W. D. G. no. 518, on stems of *Thalictrum flavum*, Tadcaster, Yorkshire, June 1950 (W. G. Bramley). In this collection the host epidermis is less uplifted than in the above. The cells of the excipulum are slightly smaller than in the type and those of the apothecial base are distinctly browner. The spore range is $18-23-(26) \times 3-4 \mu$. (Figs. 2, 6).

BELONIELLA OSILIENSIS (Vestgr.) Rehm has not been available to me but the description leaves little doubt as to its identity.

Specimens of the Yorkshire collection have been deposited at the herbarium of the Royal Botanic Gardens, Kew, and the British Museum (Natural History).

My best thanks are due to Mr Stanley Jay Smith of the New York State Museum at Albany and to Dr R. W. G. Dennis of Kew for kindly allowing me to study the relevant exsiccati.

(Accepted for publication 20 March 1953)

LIST OF BRITISH UREDINALES

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Of the 323 numbered entries (including 150*a* and 290*a*) in this list, it may be noted that nos. 1-3, 5, 68, 82, 88, 124, 140, 147, 156-7, 161, 167, 210, 215, 226, 241, 259, 262, 265-7, 271, 275, 280, 286, 292, 301, 317, 320 and 321 are doubtful, non-British, or to be deleted. The remaining 290 names might seem to be entitled to rank as British species. (Grove's book has about 263 species, including most of the thirty-three names referred to above as doubtful, etc.) We consider, however, that numbers 11-19, 119, 146-7, 199, 200, 222-4 and 282-3 are no more than forms or races. This leaves 271 names, three of which are varieties, that we consider to represent good British Uredinales. Some may prefer to place ten of these names as forms or vars. of *Puccinia rubigo-vera* (q.v.).

There is still much work to be done on the rusts of the British Isles.

For forty years Grove's *British Rust Fungi* has been the standard guide to our rusts, to the British literature up to 1913, and to the fluctuating names applied to the species during the preceding century. Grove's book is the main starting-point of this List, though references are sometimes given also to Plowright's excellent book (10) of 1889, which students of the Uredinales still find useful. Plowright listed the British exsiccati. Few references are given to Massee's hasty compilation (50) of 1913. The literature since 1913 has been examined for references to British rusts, but some papers purely plant pathological in nature are not indexed. Miss E. M. Wakefield and Dr R. W. G. Dennis have given us access to the specimens accumulated in Herb. Kew.

It is still difficult to give the distribution of most rusts over England and Wales. Some of the counties have kept careful records of rusts, notably Norfolk, home of uredinologists from Plowright to E. A. Ellis; records in 54 start with vol. 1 in 1873 and still go on. Other county lists that should be noted are those for Yorkshire (35 and 115), Suffolk (118), Hertfordshire (118A); see also 27 (1916, 52 and 1920, 37), and the numerous foray records in these *Transactions*. These county and foray records are indexed only for less common rusts and, when nothing is said about the distribution of a species, it can probably be found in most of the counties of England and Wales.

The distribution of the rusts in Scotland is known through the data published in 65, xxxi *et seq.* indexed herein. The Irish also keep track of their records of rusts (see 70 (xxv, no. 4); 71 (xxviii *et seq.*)) and, though Irish references are frequently entered here, they are not given for some of the species recorded there.

As the alternate hosts of heteroecious rusts were demonstrated, uredinologists sometimes based specific names of these rusts on the host-combination involved, regardless of morphological similarities of the rusts. This

meant that a taxonomist could name some rusts only after he had ascertained the alternate host. Grove (1913) sought to alleviate this difficulty by grouping some species of *Melampsora* and by using the name *Puccinia dispersa* sensu lat. to include several species of leaf rusts of grasses. Arthur (*Manual of the rusts of the United States and Canada*, 1934) similarly grouped these grass rusts under the name *P. rubigo-vera*. Jørstad (1952, 1951 and previous papers) has ably considered some of these problems; he (1951) accepted *P. rubigo-vera* as a collective species but used the usual binomials (*P. agropyrina*, *P. agrostidis*, *P. bromina*, *P. dispersa*, *P. triticea*, etc.) for the eleven constituent elements he found in Norway. We have generally followed Jørstad's publications whenever he has dealt with a rust found in Britain, but only under *Coleosporium* have we grouped species extensively.

The problems of nomenclature of the Uredinales have been increased by the revision of the Rules at Stockholm in 1950 to make a name based only on *Uredo* invalid for transfer as a name for the perfect state (*Puccinia*, *Uromyces*, etc.). Thus *Puccinia glumarum* [Schm.] Erikss. & Henn. (the '[Schm.]' can be omitted, as in Grove) now dates from 1894, not from 1827 as it did when *Uredo glumarum* Schm. was considered transferable to make *Puccinia glumarum* (Schm.) Erikss. & Henn. Jørstad thought that the name *P. striiformis* Westend. (1854) was probably the earliest valid name for this species; but he temporarily continued to use the name *P. glumarum*, as we do. While we have tried to check each name back to its original source and have changed some names or author citations from those used by Grove, we have thought it better not to propose any new combinations and have retained a few names that seem doubtful, with little discussion of nomenclature. Some changes in the names here used will be required eventually.

The names of hosts are taken from *Flora of the British Isles*, by Clapham, Tutin & Warburg, 1952; host names in the literature are altered when necessary without comment. Cultivated woody plants are named from Rehder's *Manual of Cultivated Trees and Shrubs* (1940), and herbs from Bailey's *Manual of Cultivated Plants* (1949) or his *Hortus Second*.

We are grateful to many mycologists for specimens or for help in preparing this list. Special thanks should be given to the late Alex. Smith, to E. A. and M. B. Ellis, and to W. G. Bramley.

Data on some of the species entered here are to be presented later by M. Wilson and D. M. Henderson. The papers sometimes referred to as 'Jørstad, 1951' or 'Jørstad, 1952' are:

JØRSTAD, I. The graminicolous rust fungi of Norway. *Skr. norske Vidensk. Akad.* **1**, no. 3, 1950, 92 pp., 1951.

JØRSTAD, I. The Uredinales of Iceland. *Skr. norske Vidensk. Akad.* **1**, no. 2, 1951, 87 pp., 1952.

The entries are numbered for precision of reference in the Host index and the List of synonyms.

An asterisk (*) indicates a figure. Grove (3) also illustrates most of the British rusts.

LIST OF SPECIES

- 1 **Aecidium hellebori** Fisch. 3, 386. One doubtful record on *Helleborus viridis*, Cheshire, 1890.
- 2 — **importatum** P. Henn. 28 (xii, 114); 65 (xxxI, 365), referred with much doubt to *Uromyces ari-virginici* Howe. On *Peltandra virginica* cult., R.B.G., Edinburgh.
- 3 — **poterii** Cooke in 27 (ii, 39*, 1864). The host of this *Aecidium* has been determined at Herb. Kew. as *Pimpinella saxifraga*, not *Poterium sanguisorba*, and the rust is *Puccinia pimpinellae* H. Mart.]
- 4 — **ranunculacearum** DC. var. **linguae** Grove in 3, 387; 65 (xxxI, 441); Ellis 54 (xiii, 498) and Bramley found indications that it is a stage of *Puccinia magnusiana*. On *Ranunculus lingua*, Scotland, 1821, and Norfolk; on *R. flammula*, Askham Bog, Yorks, amongst *Puccinia magnusiana* and its aecia on *Ranunculus bulbosus*. *Gaeoma ari-italici* (Duby) Wint. See *Melampsora allii-populina*.
- 5 ?**Calypsotheca goeppertiana** Kühn. Reported 50, 177 and 3, 372, I on *Abies alba* and *A. nordmanniana*; III on *Vaccinium vitis-idaei*, in England, Wales and Scotland; an earlier report in 71 (xxviii, 137) was from Ulster. No British specimen was found up to 1934 (see 65 (xxxI, 430)) nor has one been found by us since, in the field or in herbaria.
- 6 **Chrysomyxa abietis** Unger 65 (xxxI, 411) with references; 112, 285. III on *Picea abies* and *P. sitchensis* in Scotland and Northumberland and on *P. rubens* in Argyllshire.
- 7 — **empetri** [Pers.] Schroet. 3, 311; 65 (xxxI, 410); 71 (xl, 48). II on *Empetrum nigrum*, Scotland, North Wales, Ulster.
- 8 — **pyrolae** Rostr. 3, 312; 65 (xxxI, 410). II, III on *Pyrola minor* and *P. rotundifolia* in Scotland, rarely in England. Jørstad (1952) considers *Chrysomyxa pirolata* Wint. the correct name.
- 9 — **rhododendri** de Bary 3, 384; 27 (lv, 134); 64 (xxix, 187*); 65 (xxxI, 410); 112, 285. O, I on *Picea abies* and *P. sitchensis* Scotland; II, III on *Rhododendron hirsutum* and *R. ponticum* in Scotland and Ulster, *R. cinnabarinum* and *R. roylei* in Cornwall, *R. hippophaeoides* × *racemosum* and *R. kalecticum* in Kent, *Rhododendron* sp. in Cheshire, and to *R. keysii* by inoculation.
- 10 **Coleosporium tussilaginis** (Pers.) Lév. Since it has been found impossible to distinguish the north European 'species' of *Coleosporium* on morphological characters, we consider it best to include them as forms of one species with O, I on *Pinus sylvestris* (see Jørstad, 1952), sometimes on other pines; for two British forms O, I are unknown. It generally is possible to give the old names from the hosts of II and III as given below. *Coleosporium tussilaginis* in the restricted sense has been recorded 3, 322; 65 (xxxI, 413); 70 (1949, 39) on *Pinus sylvestris*; II, III common on *Tussilago farfara*; on *Euryops evansii*, Kew, 1953.
- 11 As *Coleosporium cacaliae* Fuckel: 3, 325; 65 (xxxI, 414). O, I not known in Britain; II, III rare on *Cacalia* [? *Senecio*] *hastata* and *C. suaveolens*, both cult.
- 12 As *Coleosporium campanulae* Lév.: 3, 328; 54 (xiii, 504); 65 (xxxI, 415); 70 (1949, 39). O, I on *Pinus sylvestris*; II, III on *Campanula glomerata*, *C. latifolia*, *C. rotundifolia*, *C. trachelium*, *C. persicifolia* cult., *C. carpatica* var. *turbinata* cult.
- 13 As *Coleosporium euphrasiae* Wint.: 3, 326 (with *C. melampyri* under *C. rhinanthacearum*); 65 (xxxI, 414); 70 (1949, 39). O, I on *Pinus sylvestris*; II, III on *Euphrasia officinalis* agg., *Odontites verna*, *Parentucellia viscosa*, *Rhinanthus minor* agg., *R. 'crista-galli'*.
- 14 As *Coleosporium melampyri* Karst.: 3, 327; 48 (ix, 184); 65 (xxxI, 414); 118, 9. O, I on *Pinus sylvestris*; II, III on *Melampyrum arvense*, *M. pratense* and its var. *montanum*.
- 15 As *Coleosporium narcissi* Grove in 27 (1922, 121). Known only from one collection of II on *Narcissus majalis* in Lincolnshire.
- 16 As *Coleosporium petasitis* Lév.: 3, 323; 28 (ix, 142); 54 (xv, 372); 65 (xxxI, 414). O, I on *Pinus sylvestris* and *P. nigra* subsp. *laricio*; II, III on *Petasites albus*, *P. hybridus*, *P. japonicus* and *P. palmatus* cult.

- 17 As *Coleosporium senecionis* Fr.: 3, 320; 10, 248*; 28 (ix, 141); 54 (xiii, 504, xvi, 174); 65 (xxxi, 413); 70 (1936, 392); 79 (vi, 23); 112, 289*. O, I on *Pinus sylvestris*, *P. nigra* and its subsp. *laricio*; II, III on *Senecio congestus* var. *palustris*, *S. jacobaea*, *S. squaridus*, *S. sylvaticus*, *S. viscosus*, *S. vulgaris*, and the cult. or escaped *S. cruentus*, *S. fluviatilis*, *S. moorei*, *S. smithii*, *Calendula officinalis*, perhaps this form on *Chrysanthemum carinatum*, and on *Notonia grandiflora* in Kew Gardens in 1894.
- 18 As *Coleosporium sonchi* Lév.: 3, 324; 32 (xiii, 184); 48 (ix, 184); 65 (xxxi, 414); 70 (1936, 392). O, I on *Pinus sylvestris*; II, III on *Sonchus arvensis*, *S. asper*, *S. oleraceus* and *S. palustris*.
- 19 As *Coleosporium tropaeoli* (Desm.) Palm: 27 (1932, 112); 3, 386 as *Uredo tropaeoli* Desm.; 35 (1914, 148); 115, 44 as '*Hemileia tropaeoli* Desm.'. II recorded on *Tropaeolum peregrinum*, Shere in Surrey, Yorkshire and Guernsey.
- 20 **Cronartium flaccidum** (Alb. & Schw.) Wint. 10, 254; 54 (xiii, 503); 3, 313 as *C. asclepiadeum* Fr.; 28 (xx, 6); 112, 285. I on *Pinus sylvestris*, Devon, 1927, in Herb. Kew.; II, III on *Paeonia officinalis* in Norfolk before 1889 and in Herb. Kew. from Crawley, Sussex, 1924; on *Tropaeolum majus* cult., Norfolk, 1934.
— *quercuum* Miyabe. See *Uredo quercus*.
- 21 — **ribicola** J. C. Fisch. 3, 316; 28 (vii, 83; xii, 114); 54 (xiii, 503); 65 (xxxi, 412); 79 (i, v, et seq.); 85 (xxxv, 22); 112, 283*. O, I on *Pinus ayacahuite*, *P. cembra*, *P. griffithii*, *P. lambertiana*, *P. monticola*, *P. parviflora*, *P. strobus*; II, III on *Ribes nigrum*, *R. rubrum*, *R. sanguineum*.
- 22 **Cumminsia mirabilissima** (Peck) Nannf. 65 (xxviii, 164, 1923) as *Puccinia mirabilissima* Peck, first European record; III spores and their pedicels ejected forcibly; 28 (ix, 135); 54 (xiii, 491); 65 (xxxi, 405); 71 (xlii, 48); 85 (xxix, 16); *Ann. mycol., Berl.*, xxviii, 225, aecia reported. O, I, rare, II, III common on *Mahonia aquifolium*.
- 23 **Endophyllum euphorbiae-silvaticae** (DC.) Wint. 3, 333; 32 (xxviii, 162); 54 (xiii, 503). O, III rare on *Euphorbia amygdaloides* in England.
- 24 — **sempervivi** (Alb. & Schw.) de Bary 3, 335; 10, 230; 28 (xix, 240); 65 (xxxi, 415); 112, 290*. O, III on *Sempervivum tectorum* and *Sempervivum* spp.
- 25 **Frommea obtusa** (Str.) Arth. 115, 44; 3, 301 as *Kuehneola tormentillae* (Fuckel) Arth.; 54 (xiii, 501); 65 (xxxi, 409); 70 (1949, 39). O, II, III on *Potentilla erecta* and *P. reptans*.
- 26 **Gymnosporangium clavariiforme** (Pers.) DC. 3, 304; 54 (xiii, 502); 65 (xxxi, 409); 112, 282. O, I on *Crataegus monogyna*, *C. oxyacanthoides*, *Pyrus communis*; III on *Juniperus communis*.
- 27 — **confusum** Plowr. in 10, 232*; 3, 306; 28 (xxviii, 13*); 54 (xiii, 502). O, I on *Crataegus monogyna*, *C. oxyacanthoides*, *Cydonia oblonga*, *Mespilus germanica*; III on *Juniperus sabina* cult.
- 28 — **fuscum** DC. 3, 308 as *G. sabinae* [Dicks.] Wint.; 65 (xxxi, 409); 79 (xii, 31). O, I on *Pyrus communis*; III on *Juniperus sabina* cult. *Gymnosporangium fuscum* DC. (1805) appears to be the first valid name applied to this rust.
- 29 — **juniperi** Link 3, 307; 65 (xxxi, 409). O, I on *Sorbus aucuparia*; III on *Juniperus communis*, Scotland, rarely in England.
[*Hemileia* spp. See under *Uredo*.]
- 30 **Hyalopsora aspidiotus** Magn. 3, 374; 65 (xxxi, 431). II, III on *Thelypteris dryopteris*, Scotland.
- 31 — **polypodii** (Diet.) Magn. 3, 375; 54 (xv, 372); 65 (xxxi, 432); 115, 43. II, III on *Cystopteris fragilis*, Scotland, Wales, Westmorland, Yorkshire and Norfolk etc.
Kuehneola tormentillae, see *Frommea obtusa*.
- 32 **Kuehneola uredinis** (Link) Arth. 112, 281; 3, 300 as *Kuehneola albida* (Kühn) Magn.; 54 (xiii, 501); 65 (xxxi, 408). O, II, III on *Rubus fruticosus* agg.
- 33 **Melampsora allii-fragilis** Kleb. 3, 344; 65 (xxxi, 418); 70 (1949, 39). O, I on *Allium cepa*, *A. ursinum*, *Allium* spp.; II, III on *Salix fragilis* and *S. pentandra*. Aecia of this and the next two species on *Allium* cannot be named with certainty without a clue to the telial host.
- 34 — **allii-populina** Kleb. 3, 347 (under *M. populina* Lév.); 65 (xxxi, 422). O, I on *Allium cepa*, *A. ursinum*, *Allium* spp.; II, III on *Populus nigra*, *P. trichocarpa*,

Populus spp. Cruchet (Bull. Soc. vaud. Sci. nat. LVI, 485, 1928) found that *Caecoma ari-italici* (Duby) Wint. on *Arum maculatum* belongs here; there is one British record (see 3, 388) near Salisbury in 1897.

- 35 **Melampsora allii-salicis-albae** Kleb. 3, 345; 65 (xxxI, 419); 112, 286; 54 xiv, 106) as *Melampsora salicis-albae* Kleb. O, I on *Allium ursinum*, *Allium* spp.; II, III on *Salix alba* and its var. *vitellina*.
- 36 — **amygdalinae** Kleb. 28 (iv, 105); 78 (1931, 133*); 112, 286. An autoecious species on *Salix* in Scotland and on *S. triandra* in Somerset and elsewhere.
- 37 — **epitea** Thuem. 10, 239; 3, 340 as *Melampsora larici-epitea* Kleb.; 65 (xxxI, 416); 70 (1936, 393); 78 (1931, 137); 112, 286; 118, 10. I on *Larix decidua*; II, III on *Salix alba*, *S. atrocinerea*, *S. aurita*, *S. caprea*, *S. ?fragilis*, *S. hippophaëfolia*, *S. nigricans*, *S. phylicifolia*, *S. purpurea*, *S. repens*, *S. smithiana*, *S. ?triandra*, *S. viminalis*. As *Melampsora alpina* Juel: 27 (1915, 48; 1919, 161); 28 (iv, 105; v, 241); 65 (xxxI, 420). O, I on *Saxifraga oppositifolia*, II, III on *Salix herbacea*, Scottish mountains. As *Melampsora arctica* Rostr. and *Caecoma saxifragarum* (DC.) Wint.: 3, 346; 65 (xxxI, 419 and 421); 115, 43; 28 (ix, 142). O, I on *Saxifraga hypnoides*, II on *Salix herbacea*, Scotland and Yorkshire.
- 38 — **epitea** var. **reticulatae** (Blytt) Jørst. 28 (ix, 139) as *Melampsora reticulatae* Blytt; 65 (xxxI, 421). O, I on *Saxifraga aizoides*, II, III on *Salix reticulata*, Scotland.
- 39 — **euonymi-caprearum** Kleb. 3, 339; 65 (xxxI, 416); 118, 10. O, I on *Euonymus europaeus*, occasional in England; II, III on *Salix atrocinerea*, *S. caprea*, *S. cinerea*, England and Scotland.
- 40 — **euphorbiae** Cast. 3, 353; 48 (ix, 184); 54 (xiii, 502); 65 (xxxI, 423); 70 (1936, 393). I rare and II, III common on *Euphorbia exigua*, *E. helioscopia*, *E. hyberna*, *E. peplus*.
- 41 — **euphorbiae-dulcis** Otth 28 (xviii, 273). II, III on *Euphorbia dulcis*, Glengariff, Eire.
- 42 — **hypericorum** Wint. 3, 354; 65 (xxxI, 423); 70 (1936, 393); 79 (xv); 118, 10. O, I unknown (fide Dietel); II, III on *Hypericum androsaemum*, *H. dubium*, *H. elatum*, *H. humifusum*, *H. perforatum*, *H. pulchrum*, *H. ?tetrapterum*. This rust is often called *Mesopsora hypericorum* (Wint.) Diet.
- 43 — **larici-caprearum** Kleb. 3, 338; 54 (xiii, 502); 65 (xiii, 416). I on *Larix decidua* and *L. leptolepis*; II, III on *Salix atrocinerea*, *S. aurita*, *S. caprea*, *Salix* spp. see 3, 345. I on *Larix decidua*; II, III on *Salix pentandra*, Scotland.
- 44 — **larici-pentandrae** Kleb. 27 (1921, 314 as 'salici-pentandrae'); 65 (xxxI, 417); 70 (1936, 393); 112, 287. I on *Larix decidua* and *L. leptolepis*; II, III on *Populus canadensis*, *P. candicans*, *P. generosa*, *P. italica*, *P. laurifolia*, *P. nigra*, *P. robusta*, *P. tremula*, *P. trichocarpa*.
- 45 — **larici-populina** Kleb. 3, 348 (under *Melampsora populina* Lév.); 65 (xxxI, 422); 70 (1936, 393); 112, 287. I on *Larix decidua* and *L. leptolepis*; II, III on *Populus canadensis*, *P. candicans*, *P. generosa*, *P. italica*, *P. laurifolia*, *P. nigra*, *P. robusta*, *P. tremula*, *P. trichocarpa*.
- 46 — **lini** (Ehrenb.) Lév. 3, 355; 23 (L, 16); 65 (xxxI, 423); 79 (v and xi); 112, 287; Muskett & Colhoun, *Diseases of Flax*, p. 25. O, I, II, III on *Linum catharticum* and *L. usitatissimum*.
- 47 — **repentis** Plowr. 54 (xiii, 502); 3, 343 as *Melampsora orchidis-repentis* Kleb.; 65 (xxxI, 417); 71 (xxxI); 118, 10. O, I on *Gymnadenia conopsea*, *Listera ovata*, *Orchis praetermissa*, *Orchis* sp.; II, III on *Salix aurita* and *S. repens*.
- 48 — **ribesii-purpureae** Kleb. 3, 342; 28 (iv, 105); 118A, 169; see 61 (xxxI, 442); possibly 10, 239 p.p. as *Melampsora mixta*. O, I on *Ribes alpinum* and *R. wacrispa* (British records doubtful); II, III on *Salix purpurea*, Hertfordshire and perhaps elsewhere.
- 49 — **ribesii-viminalis** Kleb. 3, 342; 65 (xxxI, 417). II, III rare on *Salix viminalis*, Scotland (and England?); O, I on *Ribes*, apparently not recorded here.
- 50 — **tremulae** Tul. 3, 349 and as *Melampsora larici-tremulae* Kleb.; 65 (xxxI, 422); 115, 43. I on *Larix decidua*, II, III on *Populus alba* and *P. tremula*. As *Melampsora pinitorqua* Rostr.: 3, 350; 76 (1944, 47); 112, 286; 115, 44. O, I on *Pinus sylvestris*; II, III on *Populus tremula*, Sussex, Kent, Lincolnshire and Yorkshire. As *Melampsora rostrupii* Wagner: 3, 351; 54 (xiii, 502); 65 (xxxI, 423); 112, 287; 115, 44. O, I on *Mercurialis perennis*; II, III on *Populus alba* and *P. tremula*.
- 51 — **vernalis** Niessl 3, 357; 65 (xxxI, 424). O, I, ?II, III on *Saxifraga granulata*, Scotland.

- 52 **Melampsorella caryophyllacearum** Schroet. 3, 363; 27 (1920, 39); 28 (vii, 83; ix, 140; xii, 114); 54 (vii, 255; xiii, 502); 65 (xxxI, 426); 70 (1936, 394); 112, 288 as *M. cerastii* (Pers.) Schroet. O, I on *Abies alba* and *A. nordmanniana*; II, III on *Cerastium arcticum*, *C. arvense*, *C. ?glomeratum*, *C. semidecandrum*, *C. tomentosum*, *C. vulgatum*, *Stellaria graminea*, *S. holostea*, *S. media*.
- 53 — **symphyti** Bub. 3, 363; 28 (xviii, 274); 65 (xxxI, 426); 71 (xlii, 49). II on *Symphytum officinale* and *S. tuberosum*; II, III on *S. peregrinum*. I on *Abies* not recorded here.
- 54 **Melampsorium betulinum** (Desm.) Kleb. 3, 358; 48 (ix, 184); 65 (xxxI, 424); 112, 288. O, I on *Larix decidua* and *L. leptolepis*; II, III on *Betula pubescens* and *B. verrucosa*.
- 55 — **hiratsukanum** Itô. Hiratsuka, *Mem. Tottori agric. Coll.* iv, 194; 28 (ix, 140) as *M. alni* (Thuem.) Diet.; 27 (1921, 315); 65 (xxxI, 425); 70 (1936, 393). II, III on *Alnus glutinosa* and *A. incana*.
- 56 **Milesia blechni** (Syd.) Arth. 28 (xx, 117); 54 (xiii, 503), 70 (1949, 40); 3, 377 as *Milesina blechni* Syd.; 65 (xxxI, 435); 71 (xlii, 49). O, I on *Abies alba*, II, III on *Blechnum spicant*. *Milesia* is accepted instead of *Milesina* on the basis of Rogers's statements in *Mycologia*, xl, 251, 1948.
- 57 — **carpatica** (Wrobl.) Faull 28 (xx, 117). II, III on *Dryopteris filix-mas*, Devon.
- 58 — **kriegeriana** (Magn.) Arth. *J. Arnold Arbor.* xvii, 26; 28 (xx, 116); 54 (xv, 129); 65 (xxxI, 433) as *Milesina kriegeriana* Magn.; 28 (ix, 142) as *Aecidium pseudocolumnare* Kühn; 70 (1936, 395). O, I on *Abies alba*, *A. cephalonica*, *A. nordmanniana*, and on *A. grandis* in Ulster in 1952; by inoculation on *A. concolor* and *A. grandis*; II, III on *Dryopteris austriaca*, *D. filix-mas*, *D. spinulosa*; Scotland, Ireland, Devon, Hampshire, Norfolk, etc.
- 59 — **murariae** (Syd.) Faull 28 (xx, 118); 48 (ix, 184); 70 (1936, 394); 27 (1921, 311) as *Milesina murariae* Syd.; 65 (xxxI, 434). II on *Asplenium ruta-muraria*, Scotland and Ireland.
- 60 — **polypodii** B. White *J. Arnold Arbor.* xvii, 26; 28 (xx, 116); 70 (1949, 40); 3, 376 as *Milesina dieteliana* Magn.; 27 (1916, 54); 65 (xxxI, 436). O, I by inoculations on *Abies alba* and *A. concolor*; II, III on *Polypodium vulgare*.
- 61 — **scolopendrii** (Fuckel) Arth. *J. Arnold Arbor.* xvii, 26; 28 (xx, 117); 70 (1949, 40); 3, 378 as *Uredo scolopendrii* (Fuckel) Schroet.; 65 (xxxI, 436). O, I by inoculations on *Abies alba* and *A. concolor*; II, III on *Phyllitis scolopendrium*.
- 62 — **vogesiaca** (Syd.) Faull *J. Arnold Arbor.* xvii, 26; 28 (xx, 116); 70 (1949, 40). O, I by inoculation on *Abies alba*; II, III on *Polystichum setiferum*, Eire.
- 63 — **whitei** Faull 28 (xx, 118); 27 (lix, 109) in error as *Milesina polystichi* (Wine-land) Grove; 65 (xxxI, 434). II, III on *Polystichum setiferum*, Scotland, Eire and Devon.
- 64 **Nyssopsora echinata** (Lév.) Arth. 65 (xxxiii, iv). III on *Meum athamanticum*, Glen Lyon and Lawers, Scotland. The specimen recorded in *Blumea*, Suppl. 1, p. 147, is presumably British.
- 65 **Ochropsora ariae** (Fuckel) Ramsb. in 28 (iv, 337, 1914); 3, 329 as *O. sorbi* Diet.; 65 (xxxI, 415); 79 (v, xi); 28 (xxiv, 109*) as *Aecidium leucospermum* DC. O, I on *Anemone nemorosa*; II, III on *Sorbus aucuparia* not reported here, though there is an unverified report of III on crab apple in Wales.
- 66 **Peridermium pini** (Pers.) Lév. 65 (xxxI, 412); 112, 285. Repeating I on *Pinus sylvestris*, Scotland, Ireland, Norfolk and Suffolk.
- 67 **Phragmidium fragariastris** (DC.) Schroet. 3, 290; 28 (xi, 16); 54 (xiii, 501); 48 (ix, 184); 65 (xxxI, 406). O, I, II, III on *Potentilla erecta*, *P. reptans*, *P. sterilis*. As noted 28 (iv, 335), *Phragmidium fragariae* (DC.) Wint. has priority; but everyone has followed de Candolle, who in 1815 rejected his misleading epithet.
- 68 — **fusiforme** Schroet. 3, 294; 65 (xxxI, 407). One doubtful record on introduced *Rosa pendulina*. No British specimen known.]
- 69 — **murconatum** (Pers.) Schl. 28 (iv, 338, xiv, 169); 34 (xxv, 730); 54 (xiii, 501); 79 (vii, xi); 82 (1933-6); 112, 280*; 118, 8; 3, 293 as *P. disciflorum* (Tode) James; 65 (xxxI, 407). O, I, II, III on *Rosa canina*, *R. involuta*, *R. laxa*, *R. rubiginosa*, *R. rugosa*, *R. spinosissima*, *R. tomentosa*, *R. villosa*, *Rosa* spp.

- 70 **Phragmidium potentillae** (Pers.) Karst. 3, 291; 65 (xxxI, 406); 70 (1936, 391). O, I, II, III on *Potentilla anglica*, *P. argentea*, *P. verna*, *Potentilla* spp. cult.
- 71 — **rubi** (Pers. ex Sow.) Wint. 3, 297; 10, 224*; 54 (xiii, 501); 65 (xxxI, 407). O, I, II, III on *Rubus* spp.
- 72 — **rubi-idaei** (DC.) Karst. 3, 298; 54 (xiii, 501); 65 (xxxI, 408); 79 (I, 30) *et seq.* O, I, II, III on *Rubus idaeus*.
- 73 — **rubi-saxatilis** Liro 65 (xxxI, 407); see 3, 297. I, II, III on *Rubus saxatilis*, Scotland.
- 74 — **sanguisorbae** (DC.) Schroet. 3, 292; 32 (iii, 184); 70 (1936, 391); 118, 8. O, I, II, III on *Poterium sanguisorba*.
- 75 — **violaceum** (Schultz) Wint. 3, 295; 54 (xiii, 501); 65 (xxxI, 407); 70 (1949, 39); 79 (iii, 25) *et seq.* O, I, II, III on *Rubus fruticosus* agg. and *R. laciniatus* cult.
- 76 **Puccinia absinthii** DC. 3, 134; 54 (xiii, 493); 65 (xxxI, 368). [O], II, III on *Artemisia absinthium*, *A. maritima*, *A. vulgaris*.
- 77 — **acetosae** Körn. 3, 223; 54 (xiii, 495); 65 (xxxI, 386); 70 (1936, 389). II, III on *Rumex acetosa* and *R. acetosella*.
- 78 — **adoxae** Hedw. f. 3, 160; 32 (xii, 95); 54 (xiii, 493); 65 (xxxI, 375); 118, 5; 118A, 170. III on *Adoxa moschatellina*.
- 79 — **aegopodii** H. Mart. 3, 185; 54 (xiii, 492); 65 (xxxI, 380). III on *Aegopodium podagraria*.
- 80 — **aegra** Grove in 27 (xxi, 274); 3, 202; 54 (xiii, 491); 79 (xi, 57, 59); 65 (xxxI, 382, xxxII, 558) as *Puccinia depauperans* Syd. O, I, II, III on *Viola cornuta*, *V. lutea*, *V. tricolor* agg., *Viola* spp. cult. *Puccinia aegra* is possibly a form of *P. violae*.
- 81 — **aethusae** H. Mart. 3, 190; 65 (xxxI, 380); 118, 5; 54 (xiii, 492) as *P. petroselini* (DC.) Lindr. O, II, III occasional in England on *Aethusa cynapium* and *Petroselinum crispum*. This rust is by some considered to belong with *Puccinia bullata*.
- 82 [— **agropyri** Ell. & Everh. 3, 281; 10, 265 as *Aecidium clematidis* DC. O, I on *Clematis vitalba*, fide Plowright; no recent record and none of II or III on *Agropyron*.]
- 83 — **agropyrina** Erikss. 3, 263; 65 (xxxI, 399). II, III on *Agropyron caninum* and *A. repens*. See *Puccinia rubigo-vera*.
- 84 — **agrostidis** Plowr. 3, 275; 65 (xxxI, 403); 130, 14. O, I on *Aquilegia vulgaris*, Sussex, Worcestershire, Cumberland and Aberdeenshire; II, III on *Agrostis stolonifera* and *A. tenuis*. See *Puccinia rubigo-vera*.
- 85 — **airae** [Lagerh.] Mayor & Cruchet 35 (1942, 46) as *Uredo airae* Lagerh.; 65 (xxxI, 440); see 3, 265 and 28 (vii, 82; xi, 7) under *Puccinia dispersa* sensu lat. II occasional on *Deschampsia caespitosa* (and *D. flexuosa*?).
- 86 — **albescens** Plowr. in 10, 153; 3, 162; 54 (xiii, 493); 65 (xxxI, 375). O, I, occasional, II, III rare on *Adoxa moschatellina*.
- 87 — **albulensis** Magn. 65 (xxxI, 377) as *Puccinia porteri* Peck. III on *Veronica alpina*, Braemar and (see *Puccinia veronicarum*) elsewhere in Scotland.
- 88 — **allii** Rud. 22, Bull. 139, p. 47, 1948. On *Allium sativum* from Portugal and perhaps in a garden in Kent; possibly this rust on *A. vineale* in Scotland.
- 89 — **ammophilina** [Kleb.] Mains 27 (1921, 313) as *Uredo ammophilina* Kleb.; 35 (1946, 157); 54 (xiii, 498); 65 (xxxI, 439); 118, 10. II on *Ammophila arenaria*, Wales, Scotland, Devon, Norfolk to Yorkshire; and III in Suffolk. Jørstad (1950) considered *Puccinia ammophilina* a syn. of *P. pygmaea*. See *Rostrupia ammophilae*.
- **andersoni** Berk. & Br. = *Puccinia cnici-oleracei*.
- 90 — **angelicae** Fuckel 3, 192; 54 (xiii, 492); 65 (xxxI, 380); 70 (1949, 37); 115, 46; 118A, 170. O, II, III on *Angelica sylvestris*.
- 91 — **annularis** (Strauss) Schl. 3, 175; 48 (ix, 184); 54 (xiii, 495); 65 (xxxI, 379). III on *Teucrium scorodonia*.
- 92 — **anthoxanthi** Fuckel 3, 269; 27 (1915, 47; 1921, 313); 28 (ix, 138); 65 (xxxI, 401); 115, 46; 130, 13. II, III on *Anthoxanthum odoratum*. See *Uredo anthoxanthina* under *Puccinia poae-nemoralis*.

- 93 **Puccinia antirrhini** Diet. & Holw. **23** (xl, 486; xli, 337); **28** (xviii, 349); **31** (xciv, 131); **54** (xiii, 494); **56** (lxi et seq.); **77** (1934, 146); **79** (x, 33, 39); **85** (xxxiii et seq.); **112**, 265. II, III on *Antirrhinum majus*.
- 94 — **apii** Desm. **3**, 184; **54** (xiii, 492); **65** (xxxi, 380); **115**, 46. O, I, II, III on *Apium graveolens*, Wales, Balnamoon in Scotland, Norfolk to Yorkshire, etc.
- 95 — **arenariae** (Schum.) Wint. **31** (no. 3371, p. 63); **54** (xiii, 491; xiv, 478; xvii, 138); **79** (xii, 32); **112**, 267; **3**, 218 as *Puccinia lychnidearum* Link; **65** (xxxi, 385); **70** (1936, 389); **79** (iv, viii); **85** (xxvii, 87; xxxvii, 19); **118**, 6; **3**, 221 as *P. saginae* Schm. & Kunze; **27** (1938, 89); **65** (xxxi, 385). III on *Arenaria serpyllifolia*, *Cerastium vulgatum*, *Cucubalus baccifer*, *Dianthus barbatus*, *D. deltoideus*, *Gypsophila elegans*, *Melandrium album*, *M. rubrum*, *Moehringia trinervia*, *Sagina intermedia*, *S. maritima*, *S. nodosa*, *S. procumbens*, *S. saginoides*, *Spergula arvensis*, *Stellaria alsine*, *S. graminea*, *S. holostea*, *S. media*, *S. nemorum*, *S. palustris*.
- 96 — **argentata** (Schultz) Wint. **3**, 204. II, III on *Impatiens capensis* and *I. nolitangere* in Surrey before 1913; on *I. capensis* in Surrey in September 1945, coll. N.Y. Sandwith.
- 97 — **arrenatheri** (Kleb.) Erikss. **3**, 284; **65** (xxxi, 401); **71** (xl, 48); **115**, 47; **118A**, 170; **130**, 13. I on *Berberis vulgaris*, Wooler, Northumberland, coll. R. W. G. Dennis; II, III widespread on *Arrhenatherum elatius*. Jørstad (1950) placed this rust under *Puccinia poae-nemoralis*.
- 98 — **asparagi** DC. **3**, 233; **23** (xl, 800); **28** (xviii, 350; xxv, 268); **54** (xiii, 495); **65** (xxxi, 390); **84** (1935, 119); **112**, 268. O, I, II, III on *Asparagus officinalis*, occasional in England; recorded once in Scotland in 1824.
- 99 — **asperulae-odoratae** Wurth **3**, 163; **27** (1920, 38); **65** (xxxi, 375); **115**, 45. I, II, III not common on *Asperula odorata*. Grove thought it very near to *Puccinia punctata*, but Gäumann (*Ber. Schweiz. bot. Ges.* XLVIII, 318) recognized several rusts on *Asperula*.
- 100 — **asteris** Duby **28** (iv, 334); **54** (xiii, 493); **3**, 129 as *Puccinia tripolii* Wallr.; **35** (1946, 157); **65** (xxxi, 368); **70** (1949, 36). III on *Aster tripolium*, Scotland, Ireland, Norfolk to Yorkshire, etc. The rusts on *Aster* spp. are variable, but some of the differences Grove mentions are due to host characters; stomata are amphigenous in *A. tripolium* and the sori, arising below stomata, are also amphigenous. See also *Puccinia leucanthemi*.
- 101 — **bardanae** Corda **3**, 138; **54** (xv, 371). On *Arctium minus* and *A. vulgare*, apparently not on *A. lappa*. The only British specimens known to us were those found abundantly in Norfolk by E. A. Ellis in 1940, in Kent by S. P. Wiltshire in 1945, and in east Suffolk by E. A. Ellis in 1950–1, though Plowright **10**, 185 records a rust on *Arctium*.
— *baryi* [Berk. & Br.] Wint., see *Puccinia brachypodii*.
- 102 — **behenis** Otth **3**, 222; **27** (1920, 38); **28** (xxxiv, 253); **54** (xv, 208); **115**, 46; **118**, 6; **65** (xxxi, 385) as *Puccinia silenes* Schroet. O, I, II, III on *Melandrium album*, *M. rubrum*, *Silene cucubalus*, *S. maritima*, Scotland, Wales, Somerset, Essex to Yorkshire, etc.
- 103 — **betonicae** DC. **3**, 174; **54** (xvi, 80); **65** (xxxi, 378); **115**, 46; **118A**, 170. III on *Stachys officinalis*, eastern England, etc.
- 104 — **bistortae** DC. **10**, 192; **3**, 225 as *Puccinia conopodii-bistortae* Kleb.; **65** (xxxi, 386); **115**, 46; **3**, 226, as *P. polygoni-vivipari* Karst.; **27** (1919, 162); **65** (xxxi, 388). I on *Conopodium majus*; II, III on *Polygonum bistorta* and *P. viviparum*, Yorkshire, Westmorland and Scotland.
- 105 — **borealis** Juel **27** (1915, 44; 1919, 162); **28** (v, 240); **65** (xxxi, 400). I on *Thalictrum alpinum*; [II, III on *Anthoxanthum odoratum*, not found in Britain]. See *Puccinia rubigo-vera*.
- 106 — **brachypodii** Otth **28** (iv, 334); **3**, 280 as *Puccinia baryi* Wint.; **54** (xiii, 498); **65** (xxxi, 404); **70** (1936, 391). II, III on *Brachypodium pinnatum* and *B. sylvaticum*.
- 107 — **bromina** Erikss. **3**, 262; **65** (xxxi, 398); **112**, 274; **115**, 47; **54** (xiii, 498) as *Puccinia symphyti-bromorum* F. Müll. II, III on *Anisantha sterilis*, *Bromus mollis*, *Bromus* spp., *Festuca gigantea*. Grove lists O, I on *Symphytum officinale*, but we have seen no British specimen. See *Puccinia rubigo-vera*.

- 108 **Puccinia bulbocastani** Fuckel 3, 186; 35 (1930, 22); 118A, 170. O, I, III on *Bunium bulbocastanum*, Dunstable, Beds, in 1896; in Yorkshire; at Harpenden, Herts, regularly.
- 109 — **bullata** (Pers.) Wint. 3, 193; 54 (xiii, 492, xvi, 173). O, II, III on *Peucedanum palustre*, Norfolk; Somerset in 1883 and (coll. N. Y. Sandwith) in 1950; III on *Selinum carvifolia*, Cambridgeshire in 1946, coll. J. P. M. Brenan and in 1950, coll. E. A. Ellis. *Puccinia silai* Fuckel is a form of *P. bullata*; see 3, 191, 118, 6. O, II, III on *Silaum silaus*, Pontrilas in Wales, Suffolk, etc.
- 110 — **bupleuri** Rud. 3, 189; 10, 154. II, III on *Bupleurum tenuissimum* in north Essex, 1887; I and III in south Essex, 1946, coll. Sandwith and Brenan; one recent collection in Suffolk.
- 111 — **buxi** DC. 3, 205; 48 (ix, 184); 65 (xxxix, 382); 79 (x, 39). III on *Buxus sempervirens*.
- 112 — **calthae** Link 3, 216; 54 (xiii, 491); 65 (xxxix, 384); 70 (1936, 389). O, I, II, III on *Caltha palustris*.
- 113 — **calthicola** Schroet. 28 (iv, 336); 54 (xiii, 491); 3, 217 as *Puccinia zopfi* Wint.; 35 (1914, 148); 65 (xxxix, 384). O, I, II, III on *Caltha palustris*.
- 114 — **campanulae** Carm. ex Berk. 3, 159; 65 (xxxix, 374); 115, 45. III on *Campanula rapunculus* and *C. rotundifolia*, Scotland and Yorkshire; reported by Berkeley on *Jasione montana* in Wales and the host and rust at Kew have been verified.
- 115 — **cancellata** Sacc. & Roum. II, III on *Juncus acutus*, Harlech, Wales; Braunton, Devon, in 1952; and coll. E. A. Ellis in Guernsey and Herm, C.I., in June 1947.
- 116 — **cardui-pycnocephali** Syd. 3, 142; 28 (xxiv, 249); 54 (xiii, 493); 65 (xxxix, 369); 70 (1936, 385). II, III on *Carduus tenuiflorus* and perhaps on the introduced *C. pycnocephalus*.
- 117 — **carduorum** Jacky 3, 141; 54 (xiii, 493); 53 (*Proc.* lxiii, 179); 65 (xxxix, 369); 115, 45. O, II, III on *Carduus crispus* and *C. nutans*.
- 118 — **caricina** DC. 3, 241 as *Puccinia caricis* Rebent.; 54 (xiii, 495; xv, 208 and 427); 65 (xxxix, 391); 70 (1949, 38). O, I on *Urtica dioica* and rarely on *U. urens*; II, III on *Carex hirta*, *C. pseudocyperus*, reported but not verified on *C. acutiformis*, *C. binervis*, *C. elata*, *C. flacca*, *C. pallescens*, *C. panicea*, *C. paniculata*, *C. pendula*, *C. riparia*. The next is a form of *Puccinia caricina*; and see *P. paludosa*.
- 119 As *Puccinia pringsheimiana* Kleb.: 3, 242; 23 (xix, 428*); 34 (xxiv, 17); 65 (xxxix, 392); 70 (1949, 38); 77 (1931, 131; 1934, 146); 112, 268. O, I on *Ribes nigrum*, *R. sanguineum* cult., *R. uva-crispa*; II, III on *Carex acuta*, *C. aquatilis*, *C. nigra*, and perhaps *C. elata*.
- 120 — **caricina** var. **uliginosa** (Juel) Jørstad (1952). 3, 249 as *Puccinia uliginosa* Juel; 65 (xxxix, 394); 115, 46. I on *Parnassia palustris*, Scotland, Orkney, Ireland and Yorkshire; II, III on *Carex nigra* in Scotland.
— *caricis* Rebent. is a *nomen ambiguum*; see Jørstad, 1952.
- 121 — **carlinae** Jacky 3, 137; 118, 4. O, II, III on *Carlina vulgaris*, Cornwall, Devon, Somerset and Suffolk; two old specimens in Herb. Kew. from Kent and Angus.
— *caulincola* Schneid., see *Puccinia schneideri* and *P. ruebsaameni*.
- 122 — **celakovskyana** Bub. 3, 166; 54 (xiii, 493); 65 (xxxix, 375); 115, 45. O, II, III on *Galium cruciata*, Scotland, Kent to Yorkshire, etc. Gäumann (*Ann. mycol.*, Berl., 1937, 194) considered this a form of *Puccinia punctata*.
- 123 — **centaureae** DC. 3, 139; 32 (iii, 184); 54 (xiii, 494); 65 (xxxix, 369); 71, xxxi; 118A, 170. O, II, III common on *Centaurea nigra*, rarer on *C. scabiosa*.
- 124 ? — **cerinth-agropyrina** Tranz. The I on *Echium vulgare* mentioned 10, 168 may belong to this rust of the *Puccinia rubigo-vera* group. See *Ber. schweiz. bot. Ges.* LVII, 242.
- 125 — **chaerophylli** Purt. 3, 195; 54 (xiii, 492; xvi, 80); 65 (xxxix, 381; xxxii, 557); 71 (xlii, 48); 115, 46. O, I, II, III on *Anthriscus sylvestris*, *Chaerophyllum aureum*, *C. temulum*, *Myrrhis odorata*.
- 126 — **chondrillae** Corda 3, 151; 54 (xiii, 494); 115, 45; 65 (xxxix, 373) as *Puccinia prenanthis* Auct. I, II, III on *Mycelis (Lactuca) muralis*.

- 127 **Puccinia chrysanthemi** Roze 3, 131; 54 (xiii, 493); 56 (1951, 322); 65 (xxxI, 368); 71 (xI, 47); 79 (I, 31 *et seq.*); 80, 107; 112, 264. II, III on *Chrysanthemum indicum* and *C. morifolium* cult.
- 128 — **chrysosplenii** Grev. 3, 214; 48 (ix, 184); 65 (xxxI, 384); 71, xxxI; 115, 46. III on *Chrysosplenium alternifolium* and *C. oppositifolium*.
- 129 — **cichorii** Bellynck. 3, 148; 54 (xvii, 139); II, III on *Cichorium intybus*, Cornwall and Norfolk; Surrey coll. N. Y. Sandwith; Suffolk coll. M. Wilson 1950. See *Puccinia endiviae*.
- 130 — **cicutae** Lasch 3, 183; 54 (xiii, 492). O, I, II, III on *Cicuta virosa*, Norfolk and Suffolk.
- 131 — **circaeae** Pers. 3, 198; 65 (xxxI, 381); 70 (1936, 388); 115, 46; 118, 6. III on *Circaea alpina* and *C. lutetiana*.
- 132 — **cirsii** Lasch 3, 142; 28 (ix, 135; xxiv, 249); 54 (xiii, 493); 65 (xxxI, 370); 70 (1936, 385). O, II, III on *Cirsium acaule*, *C. dissectum*, *C. heterophyllum* and *C. palustre*.
- 133 — **cladii** Ell. & Tracy 54 (xiv, 106, 1936; xv, 129 and 208; xvi, 173). II on *Cladium mariscus* in Norfolk. This North American rust is recorded also in Georgia, U.S.S.R.
[— *clandestina* Carm. 3, 390. This was on *Solidago virgaurea*, not *Succisa pratensis*, and the rust is *Puccinia virgaureae*.]
- 134 — **clintonii** Peck 28 (xxxv, 129*, 1952). III on *Pedicularis palustris*, Ulster and *P. sylvatica*, N.W. Scotland.
- 135 — **cnici** H. Mart. 28 (xxiv, 249); 70 (1949, 36); 27 (1931, 195) as *Puccinia cirsii-lanceolati* Schroet.; 28 (xviii, 271); 48 (ix, 184); 54 (xiii, 493); 65 (xxxI, 370); see 3, 143. O, I, II, III on *Cirsium eriophorum* and *C. vulgare*.
- 136 — **cnici-oleracei** Pers. 3, 144; 65 (xxxI, 372); 70 (1949, 36); see 28 (xxiv, 248), *Puccinia andersoni* Berk. & Br. a syn.; 3, 146. III on *Cirsium heterophyllum*, Yorkshire to Scotland, and recorded on *C. dissectum* in Ireland.
- 137 — **commutata** Syd. 28 (xxix, 144*); 65 (xxxiii, iv). I, III on *Valeriana officinalis*, Mull, Scotland.
- 138 — **confinis** Syd. I on *Solidago virgaurea*; [II, III not yet found on *Trichophorum*,] Appin and Raasay, Scotland.
- 139 — **conii** Fuckel 3, 196; 54 (xiii, 492); 65 (xxxI, 381); 70 (1936, 388); 115, 46. II, III on *Conium maculatum*.
— *conopodii-bistortae* Kleb., see *Puccinia bistortae*.
- 140 — **convolvuli** Cast. 3, 175; 10, 146. II, III on *Calystegia sepium*; one record, probably in southern England, before 1889.
- 141 — **coronata** Corda 3, 253; 28 (xxxiii, 172; xxxiv, 253); 34 (xxiv, 504*; xxv, 506*; xxxI, 364); 65 (xxxI, 395); 112, 277; 130, 7; syn. *Puccinia lolii* Niels., 3, 255; 65 (xxxI, 396); syn. also *P. coronifera* Kleb. O, I on *Frangula alnus* and *Rhamnus cathartica*; II, III on *Agropyron* sp., *Agrostis stolonifera*, *A. tenuis*, *Alopecurus pratensis*, *Arrhenatherum elatius*, *Avena fatua*, *A. sativa*, *A. strigosa*, *Calamagrostis canescens*, *C. epigejos*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Festuca altissima*, *F. ovina*, *F. pratensis*, *Holcus lanatus*, *H. mollis*, *Lolium perenne*, *Phalaris arundinacea*.
- 142 — **crepidicola** Syd. 54 (xv, 129, 1940). II, III on *Crepis capillaris*, *C. taraxacifolia*, and *C. ?biennis* in Norfolk; also on *C. taraxacifolia* in Devon, coll. A. Beaumont. *Puccinia crepidis* Schroet. is recorded II, III on *Crepis capillaris* in 3, 156; 27 (1919, 163); 35 (1943, 119); 65 (xxxI, 374); 70 (1936, 386) but, since the characteristic feature of *Puccinia crepidis* is the systemic I, followed by II, III in and between the I, it seems best to consider these as *P. crepidicola* also until the British rusts on *Crepis* are restudied.
- 143 — **cyani** Pass. 3, 140; 54 (xiv, 188); 85 (xxxix, 19); 112, 265; 118, 4. O, II, III on *Centaurea cyanus* cult.
- 144 — **difformis** Kunze & Schm. 3, 168; 65 (xxxI, 376); 54 (xvi, 173) as *Puccinia ambigua* Lagerh. I, III on *Galium aparine*, Cornwall, Devon, Surrey, Kent, Norfolk and north Scotland.
- 145 — **dioicae** Magn. 3, 244; 54 (xiii, 496; xiv, 479); 65 (xxxI, 392); 70 (1936, 390). O, I on *Cirsium dissectum* and *C. palustre*; II, III in Norfolk on *Carex dioica* and *C. rostrata*. The following may be considered forms of *Puccinia dioicae* sensu lat.; see also *P. extensicola* and *P. opizii*.

- 146 As *Puccinia schoeleriana* Plowr. & Magn. **3**, 246; **65** (xxxI, 393); **115**, 46; syn. probably *P. arenariicola* Plowr., see **28** (xviii, 268); **54** (xiii, 496); **3**, 247. O, I on *Senecio jacobaea* and in 1884 (*Puccinia arenariicola*) on *Centaurea nigra*; II, III on *Carex arenaria*.
- 147 As *Puccinia silvatica* Schroet. **3**, 245; **65** (xxxI, 393); **115**, 46. O, I on *Taraxacum officinale* agg. Until II and III are found in Britain on *Carex*, the presence of this form here must remain doubtful.
- 148 — *dispersa* Erikss. & Henn. **54** (xiii, 496); syn. *Puccinia secalina* Grove in **3**, 261; **65** (xxxI, 398). O, I on *Lycopsis arvensis*, Dorset, Kent and Norfolk; II, III common on *Secale cereale*. *Puccinia dispersa* sensu lat. of Grove (and see **26A**, Bull. H 1 and **130**, 8) = *P. rubigo-vera* sensu Arthur and Jørstad.
- 149 — *endiviae* Pass. **112**, 265. II, III on *Cichorium endivia*, Cornwall and (fide Path. Lab., Harpenden) Devon. This may be the same as *Puccinia cichorii*.
- 150 — *epilobii* DC. **3**, 200; **28** (ix, 137); **65** (xxxI, 381); **70** (1936, 388). III on *Epilobium* 'alpinum', *E. hirsutum*, *E. montanum*, *E. obscurum* and *E. palustre*.
- 150a — *eutremae* Lindr. Jørstad, *Nytt Mag. Bot.* **1**, 1952, 104. III on *Cochlearia alpina*, Northumberland.
- 151 — *expansa* Link **3**, 136; **48** (ix, 184); **65** (xxxI, 369); **71** (xl, 47); **118A**, 171; syn. probably *Puccinia glomerata* Grev., **3**, 136; **54** (xiii, 493); **65** (xxxI, 369). III on *Senecio aquaticus* and *S. jacobaea*.
- 152 — *extensicola* Plowr. in **10**, 181; **3**, 248; **54** (xiii, 496); **70** (1949, 38). O, I on *Aster tripolium*; and II, III on *Carex extensa*, Norfolk in 1888, near Dublin in 1941; I on *Aster tripolium*, Looe, Cornwall, in June 1929, coll. Rilstone and Berrow, Somerset, 6 June 1953, coll. R. E. C. Ferreira. This rust is near *Puccinia dioicae*.
- 153 — *fergussonii* Berk. & Br. **3**, 203; **27** (1920, 38); **65** (xxxI, 382); **118**, 6. III rare on *Viola palustris* in England, Scotland and Wales.
- 154 — *festucae* Plowr. **3**, 257; **54** (xiii, 498); **65** (xxxI, 396); **70** (1936, 390); **112**, 278; **115**, 46; **130**, 12. O, I on *Lonicera periclymenum*; II, III on *Festuca ovina* agg. and *F. rubra* var. *arenaria*.
— *fusca* Wint., see *Tranzschelia anemones*.
- 155 — *gentianae* Link **3**, 178; **28** (vii, 81). II, III on *Gentiana acaulis* cult. and *G. verna*, Surrey, Wales, and in Herb. Kew. from Cheshire. See *Uromyces gentianae*.
- 156 — *gibberosa* Lagerh. Grove **27** (1921, 314). II with paraphyses on *Festuca ovina*. As Grove noted, this is a very dubious record. The rust may have been *Puccinia poae-nemoralis*.
- 157 — *gladioli* Cast. **22**, Bull. 126; **79** (xi, 55). On *Gladiolus* cult., Cornwall in 1924.
- 158 — *glechomatis* DC. **3**, 173; **54** (xiv, 478); **65** (xxxI, 378); **70** (1936, 387); **118A**, 171. III on *Glechoma hederacea* and possibly this rust on *Prunella vulgaris*.
— *glomerata* Grev., see *P. expansa*.
- 159 — *glumarum* Erikss. & Henn. **3**, 258; **28** (viii, 142, ix, 137, xvi, 25, xx, 265); **34** (xiv, 105, xvi, 533, xxxI, 362); **65** (xxxI, 397); **103** (v, 231, xii, 57, xxix, 399); **112**, 275; **130**, 10. II, III on *Agropyron caninum*, *A. repens*, *Brachypodium sylvaticum*, *Bromus mollis*, *Bromus* spp., *Dactylis glomerata*, *Elymus arenarius*, *Hordeum vulgare*, *Secale cereale*, *Triticum aestivum*. See *Puccinia hordei-murini*.
- 160 — *graminis* Pers. **3**, 250; **28** (viii, 142; xi, 138; xvi, 21; xix, 128); **34** (viii, 81; xxxI, 360); **35** (1948, 11); **61** (clxiii, 107); **65** (xxxI, 394; xxxvi, 48); **112**, 268*; **130**. O, I on *Berberis vulgaris* and rarely on *Mahonia aquifolium*; II, III on *Agropyron repens*, *Agrostis canina*, *A. stolonifera*, *A. tenuis*, *Alopecurus pratensis*, *Anisantha sterilis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avena fatua*, *A. sativa*, *A. strigosa*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Festuca pratensis*, *Hordeum distichon*, *H. vulgare*, *Poa pratensis*, *P. trivialis*, *Secale cereale*, *Trisetum flavescens*, *Triticum aestivum*, *Zerna ramosa*, and other grasses. For races of *Puccinia graminis* in Scotland see Batts, **28** (xxxiv, 533).
- 161 — f.sp. *phlei-pratensis* (Erikss. & Henn.) Stakm. & Piem. **130**, 9; **3**, 283 as *Puccinia phlei-pratensis* Erikss. & Henn.; **65** (xxxI, 395). II, III on *Festuca* spp., *Phleum pratensis*, and probably on *Dactylis glomerata*. See **65** (xxxvi, 53); I on *Berberis* from inoculation with III on *Phleum*.—This forma is commonly considered to be a variety.

- 162 [**Puccinia helianthi** Schw. Recorded 50, 102 on *Helianthus*. No British specimen known.]
- 163 — **heraclei** Grev. 3, 194; 65 (xxxI, 381); 70 (1949, 37); 115, 46. O, I, II, III not common on *Heracleum sphondylium*.
- 164 — **hieracii** H. Mart. 3, 158; 54 (xiii, 494); 65 (xxxI, 374; xxxII, 557); 70 (1949, 37). O, II, III on *Hieracium* spp. (cited as *H. alpinum*, *H. boreale*, *H. murorum*, *H. umbellatum*, *H. vulgatum*). See *Puccinia hypochaeridis*, *P. leontodontis* and *P. taraxaci*.
- 165 — var. **piloselloidarum** (Probst) Jørst. 54 (xiii, 494) as *P. piloselloidarum* Probst. O, II, III widespread on *Hieracium pilosella*.
- 166 — **holcina** Erikss. 3, 263; 28 (xi, 16); 54 (xiii, 497); 65 (xxxI, 398); 118, 6. II, III on *Holcus lanatus* and *H. mollis*. See *Puccinia rubigo-vera*.
- 167 — **hordei** Otth 61 (clxii, 461); 112, 274; 28 (xx, 271) as *P. anomala* Rostr.; 34 (xxvi, 56; xxxI, 364); 3, 264 as *P. simplex* (Wint.) Erikss. & Henn.; 65 (xxxI, 399). O, I on *Ornithogalum pyrenaicum*, Wiltshire; II, III common on *Hordeum vulgare*.
- 168 — ?**hordei-murini** Buchw., syn. *Puccinia hordei* Fuckel, non Otth. 28 (ix, 137) and 65 (xxxI, 397) under *P. glumarum*. II, III on *Hordeum murinum*, Scotland and Orkney.
- 169 — **hydrocotyles** Cooke 3, 181; 27 (1916, 53); 54 (xiii, 492); 65 (xxxI, 379); 70 (1936, 387). II, III rare on *Hydrocotyle vulgaris*.
- 170 — **hypochaeridis** Oudem. 3, 148; 27 (1917, 23; 1919, 163); 53 (*Proc.* LXIII, 180); 54 (xiii, 494; xvii, 139); 65 (xxxI, 372); 70 (1936, 386). II, III on *Hypochaeris radicata*, rarely on *H. glabra*. Jørstad considers this a var. of *Puccinia hieracii*.
- 171 — **hysterium** Röhl. 28 (iv, 335); 79 (v, 29); 3, 150 as *P. tragopogonis* Corda; 54 (xiii, 494); 65 (xxxI, 373); 115, 45; 118, 4; 118A, 172. O, I, II spores, III not common on *Tragopogon pratensis* and (or?) its subsp. *minor*.
- 172 — **iris** Rabenh. 3, 230; 22, *Bull.* 117; 54 (xiii, 495); 65 (xxxI, 390); 115, 46; 118A, 171. II, III on *Iris foetidissima*, *I. pseudacorus*, and especially *I. germanica* and other spp. cult. Jørstad and Roll-Hansen (*Nytt Mag. Naturvid.* B87, 1949) obtained I on *Urtica dioica* from III on *Iris sibirica* in Norway.
- 173 — **lapsanae** Fuckel 3, 147; 54 (xiii, 494); 65 (xxxI, 372); 70 (1936, 386); 118A, 171. O, I, II, III common on *Lapsana communis*.
- 174 — **lemmonieriana** Maire 28 (xii, 113); 54 (xiii, 493); 65 (xxxI, 371); syn. *Puccinia cirsii-palustris* (Desm. [as var.]) Wilson in 28 (xxiv, 249); probably syn. *P. cardui* Plowr. in 10, 216. III on *Cirsium palustre*.
- 175 — **leontodontis** Jacky 3, 149; 54 (xiii, 494); 65 (xxxI, 373); 118, 4; 118A, 171. O, II, III on *Leontodon autumnalis*, *L. hispidus* and *L. leysleri*. Jørstad and Arthur consider this and *Puccinia taraxaci* syns. of *P. hieracii*.
- 176 — **leucanthemi** Pass. 3, 133. III on *Chrysanthemum leucanthemum* in Cornwall in 1906; probably this rust on *C. segetum* in Norfolk in 1949 (54, xvii, 138). It may be only a form of *Puccinia asteris*.
- 177 — **libanotidis** Lindr. II, III on *Seseli libanotis*, Cherry Hinton, Cambridge, coll. J. P. M. Brenan 4 August 1946; also found in Sussex in 1910.
- 178 — **liliacearum** Duby. 3, 234; 61 (clxii, 461). O, III not common on *Ornithogalum pyrenaicum* and *O. umbellatum* in England and Scotland.
— *lolii* Niels. = *Puccinia coronata*.
- 179 — **longissima** Schroet. 27 (1917, 134); 65 (xxxI, 396); not *P. paliformis* Fuckel as listed doubtfully in 3, 386. II, III on *Koeleria gracilis*, Scotland and coll. Airy-Shaw near Cirencester, Gloucestershire; I on *Sedum* not recorded here.
— *lychnidearum* Link = *Puccinia arenariae*.
- 180 — **magnusiana** Körn. 3, 271; 54 (xiii, 498); 65 (xxxI, 402); 115, 47. O, I on *Ranunculus bulbosus*, *R. repens* and perhaps (see no. 4 above) on *R. lingua* and *R. flammula*; II, III on *Phragmites communis*.
- 181 — **major** Diet. 3, 157; 65 (xxxI, 374); 70 (1936, 387); 115, 45. O, I, II, III on *Crepis paludosa*.
- 182 — **malvacearum** Mont. [or Bert. ex Mont.] 3, 206; 28 (xvi, 177); 54 (xiii, 491); 65 (xxxI, 383; xxxII, 558); 70 (1936, 389); 112, 266. III on *Althaea rosea* cult., *Lavatera arborea*, *Malva moschata*, *M. neglecta*, *M. sylvestris*, *Sidalcea* sp. cult.

- 183 **Puccinia menthae** Pers. 3, 170; 31 (xcviii, 65); 48 (ix, 184); 54 (xiii, 495); 65 (xxxix, 378); 85 (xxxix, 17); 112, 265. O, I, II, III on *Calamintha ascendens*, *Clinopodium vulgare*, *Mentha aquatica*, *M. arvensis*, *M. neglecta*, *M. piperita*, *M. spicata*, *M. sylvestris*, *Origanum vulgare*, *Satureja hortensis* cult.
- 184 — **millefolii** Fuckel 3, 131; 28 (vii, 81); 54 (xiii, 493); 65 (xxxix, 368); 118, 3. III on *Achillea millefolium*.
— *mirabilissima* Peck, see *Cumminsii*ella.
- 185 — **molinae** Tul. 3, 276; 28 (vii, 82); 65, (xxxix, 403; xxxvi, 62) as *Puccinia brunellarum-molinae* Cruchet. I on *Prunella vulgaris*, II, III on *Molinia caerulea*, Scotland.
- 186 — **oblongata** (Link) Wint. 3, 238; 54 (xiii, 495); 65 (xxxix, 391); 118, 7; 28 (xviii, 271) as *Puccinia luzulae-maximae* Diet. II, III on *Luzula campestris*, *L. pilosa*, *L. sylvatica*. Some of the specimens may have been *Puccinia obscura*.— If *Caecoma oblongatum* Link did not include III, the right name for this rust may be *Puccinia luzulae* Lib. ex Cooke, 1876.
- 187 — **obscura** Schroet. 3, 236; 48 (ix, 184); 54 (xvi, 173); 65 (xxxix, 391); 115, 46. O, I on *Bellis perennis*; II, III on *Luzula campestris*.
- 188 — **obtegens** Tul. ex Fuckel 3, 145; 54 (xiii, 493); 65 (xxxix, 372); 70 (1936, 385); 28 (xxiv, 249) as *Puccinia suaveolens* (Pers.) Rostr. O, II, III common on *Cirsium arvense*.—*Puccinia obtegens* seems to be the correct name now that names based on *Uredo* are not valid for transfer.
- 189 — **opizii** Bub. 54 (xvii, 137). O, I on *Lactuca sativa* and *L. virosa*; II, III on *Carex appropinquata* and *C. paniculata*, Norfolk, 1950–3. This rust belongs to the *Puccinia dioicae* group.
- 190 — **oxyriae** Fuckel 3, 224; 65 (xxxix, 386). II, III on *Oxyria digyna*, Scotland and North Wales.
- 191 — **paludosa** Plowr. in 10, 174; 3, 248; 54 (xiii, 496); 65 (xxxix, 394). O, I on *Pedicularis palustris*; II, III on *Carex hostiana* and *C. nigra*, perhaps this rust also on *C. echinata* and *C. elata*; Norfolk, Scotland and Orkney. This is one of the *Puccinia caricina* group.
- 192 — **pazschkei** Diet. 3, 213; 28 (vii, 81); 65 (xxxix, 383; xxxii, 586); 118A, 171. An introduced rust with III on *Saxifraga* spp. cult. cited as *S. aizoon* var. *cultrata*, *S. cotyledon* var. *catheramensis*, *S. cotyledon* × *S. aizoon*, *S. hostii* and var. *rhaetica*, *S. longifolia* and *S. obrisii*.
- 193 — **perplexans** Plowr. 3, 270; 10, 179; 65 (xxxix, 402); 115, 47; 130, 13. O, I on *Ranunculus acris*; II, III on *Alopecurus pratensis*, Norfolk, Yorkshire, Scotland and Wales. See *Puccinia rubigo-vera*.
- 194 — **persistens** Plowr. in 10, 180; 3, 282; 54 (xiii, 498); 65 (xxxix, 404); 115, 47. O, I rarely found on *Thalictrum flavum* and *T. minus*; II, III proved to be on *Agropyron repens* in Norfolk in 1888, but seldom (or never?) recognized here since.
— *phalaridis* Plowr., see *Puccinia sessilis*.
- 195 — **phragmitis** (Schum.) Körn. 3, 273; 54 (xiii, 497); 65 (xxxix, 403); 70 (1936, 390); 77 (1928, 118); 79 (v, 27); 115, 47. O, I on *Rheum rhaponticum* cult., *Rumex conglomeratus*, *R. crispus*, *R. hydrolapathum*, *R. obtusifolius*; II, III on *Phragmites communis*. See *Puccinia trailii*.
- 196 — **picridis** Hazsl. 28 (vi, 327); 118, 4. II, III on *Picris hieracioides*, South Wales, Gloucestershire and Suffolk; and from east Kent in Herb. Kew., coll. N. Y. Sandwith.
- 197 — **pimpinellae** H. Mart. 3, 188; 35 (1930, 22); 65 (xxxix, 380). O, I, II, III on *Pimpinella major* and *P. saxifraga*, Scotland, Yorkshire, etc.
- 198 — **poae-nemoralis** Otth This is the species with abundant paraphyses in the uredosori, included 3, 279 in *Puccinia poarum* in part. On *Poa annua* and *P. nemoralis*, probably widespread. The following are forms of *P. poae-nemoralis* (and see *P. arrhenatheri* and *P. gibberosa*).
- 199 As *Uredo anthoxanthina* Bub. 27 (1921, 312); 54 (xiii, 498); 65 (xxxix, 438); 130, 13; see 3, 270 under *Puccinia anthoxanthi*; 28 (vii, 83; ix, 138); 115, 47 as *P. anthoxanthina* [Bub.] Gäum. II widespread on *Anthoxanthum odoratum*.
- 200 As *Uredo glyceriae* Lind [non Opiz] 28 (xii, 115); 54 (xiii, 499; xvi, 173); 65 (xxxix, 440). II on *Puccinellia maritima* and *P. rupestris*, Scotland, Norfolk, etc.; one

- record possibly this rust (as *Puccinia poarum*, see 3, 279) on *Glyceria fluitans*.—If *U. glyceriae* be treated as a species, a valid name is *Uredo glyceriae-distantis* Eriks.
- 201 **Puccinia poarum** Niels. 3, 278; 10, 168*; 48 (ix, 184); 54 (xiii, 498); 65 (xxxI, 404); 130, 12. O, I on *Tussilago farfara*; II without paraphyses, III on *Poa annua*, *P. nemoralis*, *P. pratensis* and *P. trivialis*. These grass hosts need to be checked, for the old records included *Puccinia poae-nemoralis*.
- 202 — **polygoni-amphibii** Pers. 3, 227; 54 (xiii, 495); 65 (xxxI, 389); 70 (1936, 389); 3, 228 as *Puccinia polygoni-convolvuli* DC. which, fide Sydow and Arthur, is only a race or var.; 118, 7; 118A, 171. I on *Geranium dissectum*, Yorkshire; II, III on *Polygonum amphibium*, *P. convolvulus*, *P. lapathifolium* and *P. persicaria*.
- 203 — **porri** Wint. 3, 235; 54 (xvi, 80); 65 (xxxI, 391); 70 (1936, 389); 85 (xxxv, 20); 112, 268. II, III on cult. *Allium cepa* and especially *A. schoenoprasum*, II (only?) on *A. porrum*. See *Puccinia allii* and *Uromyces ambiguus*.
- 204 — **pratensis** Blytt. 35 (1953, 94). II, III on *Helicotrichon pratense*, Yorkshire.
- 205 — **primulae** Grev. 3, 179; 10, 159; 54 (xiii, 494); 65 (xxxI, 379); 70 (1949, 37); 115, 46; 118, 5. I, II, III on *Primula vulgaris*.
— *pringsheimiana* Kleb., see under *Puccinia caricina*.
- 206 — **prostii** Moug. 27 (1915, 43); 50, 139; 53 (LVIII, 143*); 57 (VII, 219); 65 (xxxI, 390). O, III on *Tulipa sylvestris* in Roy. Bot. Gard. Edinburgh since 1914.
— *pruni-spinosae* Pers., see *Tranzschelia*.
- 207 — **pulverulenta** Grev. 3, 198; 10, 151; 65 (xxxI, 381); 70 (1936, 388); 118, 6. O, I, II, III on *Epilobium adnatum*, *E. hirsutum*, *E. montanum*, *E. palustre* and *E. parviflorum*.
- 208 — **punctata** Link 3, 164; 54 (xiii, 493); 65 (xxxI, 375); 70 (1936, 387); 118, 5. O, I, II, III on *Galium cruciata*, II, III (only?) on *G. hercynicum*, *G. mollugo*, *G. palustre*, *G. uliginosum*, *G. verum*, and a little on *G. aparine* in Norfolk in 1952, coll. E. A. Ellis. See *Puccinia celakovskiyana* and *Ann. mycol., Berl.*, xxxv.
[— *purpurea* Cooke 112, 279. On *Sorghum*, 'has been recorded in England'. This is evidently a lapsus calami, as no British specimen or other record has been traced.]
- 209 — **pygmaea** Erikss. 27 (1928, 211); 35 (1941, 3). II, III on *Calamagrostis epigejos*, Yorkshire, Worcestershire and (in Herb. Kew. coll. Brennan in 1944) Buckinghamshire. See *Puccinia ammophilina*.
- 210 — **rhodiolae** Berk. & Br. 3, 210; 65 (xxxI, 383). Three old records of III on *Sedum rosea* in Scotland. Jørstad considered the rust to be a form of *Puccinia umbilici*.
- 211 — **ribis** DC. 3, 212; 28 (I, 33); 31 (xvi, 135, cxxii, 92); 65 (xxxI, 383). Two records of III on *Ribes sativum* (*R. ? rubrum* agg.) in Moray; found recently also in Perthshire.
[— *rubigo-vera* Wint. Arthur and Jørstad consider this to be the name for a collective species of grass rusts of similar morphology, the *Puccinia dispersa* sensu lat. of Grove. Since these rusts can generally be distinguished by their hosts, we follow European custom and Jørstad (1951) in treating them as separate species. Included herein are *P. agropyrina*, *P. agrostidis*, *P. borealis*, *P. bromina*, *P. dispersa*, *P. holcina*, *P. perplexans*, *P. persistens*, *P. triseti* and *P. triticina*.]
- 212 — **ruebsaameni** Magn. III on *Origanum vulgare*, several collections, most of them by N. Y. Sandwith, in Herb. Kew. from Kent, Surrey, Buckinghamshire, and Somerset. The rust may be a var. or form of *Puccinia schneideri*.
- 213 — **rugulosa** Tranz. 27 (LIX, 16) as *P. peucedani-parisiensis* Lindr.; 50, 122. II, III on *Peucedanum officinale*, Kent.
— *saginae* Schm. & Kunze, see *Puccinia arenariae*.
- 214 — **saniculae** Grev. 3, 182; 54 (xiii, 492); 65 (xxxI, 379); 70 (1936, 387). O, I, II, III common on *Sanicula europaea*.
- 215 [— **satyrii** Syd. III on *Satyrium aureum* imported from Africa, Orchid House, Kew, 1929.]
- 216 — **saxifragae** Schl. 3, 212; 48 (ix, 184); 65 (xxxI, 383). III on *Saxifraga granulata*, *S. spathularis* (coll. Dennis), *S. stellaris*, *S. umbrosa*, Ireland, North Wales, Cumberland and Scotland.
- 217 — **schneideri** Schroet. 3, 172 as *Puccinia caulicola* Schneid. [non (Nees) Spreng., 1827]; 65 (xxxI, 378). III on *Thymus drucei* in Scotland and coll. D. Pigott in

Buckinghamshire in 1952 and on *T. pulegioides* in Norfolk. See *Puccinia ruebsaameni*.

Puccinia schoeleriana Plowr. & Magn., see under *P. dioicae*.

218 — **schoeteri** Pass. 3, 232; 56 (xxvii, 396). III on cult. *Narcissus jonquilla* and *N. majalis* in Cheshire in 1889; on *N. pseudonarcissus* in 1894; on this host it developed and persisted in the Rock Garden at Kew, 1947-9.

219 — **scirpi** DC. 3, 239; 10, 191; 28 (v, 5; xxxiii, 180); 54 (xiii, 495); 56 (xix). O, I on *Nymphoides peltatum*; II, III on *Schoenoplectus lacustris*, Huntingdonshire, Oxfordshire, Herefordshire, Suffolk, ? Norfolk.

— **secalina** Grove = *Puccinia dispersa*.

220 — **septentrionalis** Juel 27 (1915, 44); 28 (v, 240; vii, 82; ix, 137); 65 (xxxii, 387). I on *Thalictrum alpinum*; II, III on *Polygonum viviparum* at 2000-3500 ft. in Scotland; II on *P. bistorta* by inoculation with I.

221 — **sessilis** Schneid. 3, 266; 70 (1936, 390), including *Puccinia digraphidis* Soppitt, 3, 267; 115, 47. O, I rare on *Convallaria majalis* and *Paris quadrifolia*. Most uredinologists now follow Grove in considering the three names listed below to be other races of *Puccinia sessilis*. All have II, III on *Phalaris arundinacea*.

222 As *Puccinia orchidearum-phalaridis* Kleb. 3, 268; 54 (xiii, 497); 65 (xxxii, 399); 70 (1936, 390); 115, 47; 118, 8. O, I widespread on *Gymnadenia conopsea*, *Listera ovata*, *Orchis fuchsii*, *O. praetermissa* and *O. strictifolia*.

223 As *Puccinia phalaridis* Plowr. 3, 269; 54 (xiii, 497); 70 (1949, 38); 115, 47; syn. *P. ari-phalaridis* Kleb. O, I not common on *Arum maculatum*.

224 As *Puccinia winteriana* Magn. 3, 268; 54 (xiii, 497); 65 (xxxii, 399; xxxii, 556); 70 (1949, 38); 115, 47. O, I uncommon on *Allium ursinum*; II, III (as in other races) on *Phalaris arundinacea*.

— **silvatica** Schroet., see under *Puccinia dioicae*.

225 — **smyrnii** Biv.-Bernh. 3, 197; 27 (1914, 185); 70 (1936, 388); 115, 46; 54 (xiii, 492) as *P. smyrnii-olusatris* Lindr. O, I, III on *Smyrnum olusatrum*, England to Ireland, but not known in Scotland where the host is less common.

226 — **soldanellae** Fuckel 3, 180. O, I on *Soldanella alpina* cult. in Glasgow Bot. Gard. before 1836; in Herb. Kew. from Cambridge Bot. Gard. in 1926.]

227 — **sonchi** Rob. 3, 155; 27 (1936, 297); 28 (ix, 136); 54 (xiii, 494); 65 (xxxii, 373); 71, xxxi. O, II, III on *Sonchus arvensis*, *S. asper*, *S. oleraceus* and *S. palustris*.

228 — **sorgi** Schw. 22, Bull. 126 and 139; 54 (xv, 371). II on *Zea mays* cult., Norfolk in 1941, Berkshire in 1943, Wales in 1945, Middlesex about 1925 and in 1944, Yorkshire in 1952.

229 — **tanacetii** DC. 3, 135; 54 (xiii, 493); 65 (xxxii, 369); 118, 4. II, III rare on *Tanacetum vulgare*; Norfolk in 1868, Scotland in 1891, Suffolk in 1931, Essex in 1934.

230 — **taraxaci** Plowr. 3, 154; 53 (Proc. LXIII, 180); 54 (xiii, 494); 65 (xxxii, 373); 70 (1949, 37). O, II, III on *Taraxacum officinale* agg. See *Puccinia leontodontis*.

— **thalictri** Chev. = *Tranzschelia thalictri*.

231 — **thesii** Chaill. 3, 229; 10, 145; 118, 7. O, I, II, III rare on *Thesium humifusum*, south and east England.

232 — **tinctoriicola** Magn. 28 (iv, 335); 3, 139 as *Puccinia tinctoriae* Magn. [non Speng.]; 27 (1916, 52). II, III rare on *Serratula tinctoria*, London about 1865, Worcestershire and Devon.

— **tragopogonis** Corda = *Puccinia hysteriorum*.

233 — **tralii** Plowr. in 10, 176; 3, 274; 28 (xviii, 269*); 54 (xiii, 497); 65 (xxxii, 403); 70 (1949, 38); 115, 47. O, I on *Rumex acetosa*; II, III on *Phragmites communis*. This is doubtless only a race or var. of *Puccinia phragmitis*.

— **tripolii** Wallr., see *Puccinia asteris*.

234 — **triseti** Erikss. 3, 263; 54 (xiv, 188); 65 (xxxii, 399); 115, 47; 118, 8. II, III on *Trisetum flavescens*. See *P. rubigo-vera*.

235 — **tritricina** Erikss. 3, 262; 28 (viii, 142; xx, 255); 34 (xxiii, 271; xxxii, 363); 65 (xxxii, 398); 112, 273. II, III common on *Triticum aestivum*, but not common in Scotland. See *Puccinia rubigo-vera*.

236 — **tumida** Grev. 3, 187; 54 (xiii, 492); 65 (xxxii, 380); 70 (1936, 387); 118A, 172. III on *Conopodium majus*.

— **uliginosa** Juel = *Puccinia caricina* var. *uliginosa*.

- 237 **Puccinia umbilici** Guep. 3, 211; 32 (xxxv, 185); 65 (xxxi, 383); 70 (1936, 389). III on *Umbilicus rupestris*, especially in Cornwall and Devon. See *Pucciniarhodiolae*.
- 238 — **valantiae** Pers. 3, 167; 54 (xv, 209); 65 (xxxi, 376); 118, 5. III on *Galium cruciata*, *G. hercynicum*, *G. uliginosum*, and coll. A. Smith on *G. verum* in Aberdeenshire.
- 239 — **variabilis** Grev. 3, 152; 54 (xiii, 494); 65 (xxxi, 373); 118A, 172. I, II, III on *Taraxacum officinale* agg. and *T. paludosum* agg.
- 240 — **veronicae** Schroet. 3, 169; 48 (ix, 184); 65 (xxxi, 376); 115, 46. III rare on *Veronica montana*; on *V. spicata* subsp. *hybrida* at Humphrey Head, north Lancashire.
- 241 [— **veronicarum** DC. 3, 169. The Scottish specimens on *Veronica alpina* have been re-examined and are *Puccinia albulensis*.]
- 242 — **vincae** Berk. 3, 176; 10, 161; 54 (xiii, 494); 65 (xxxi, 379); 118A, 172. O, II, III rare on *Vinca major*. We have traced no British specimen on *V. minor*. *Puccinia cribrata* Arth. & Cumm., *Ann. mycol., Berl.*, 1933, is described on *Vinca minor* in Europe.
- 243 — **violae** DC. 3, 200; 65 (xxxi, 382); 70 (1936, 388); 79 (iii et seq.). O, I, II, III common on *Viola canina*, *V. hirta*, *V. odorata*, *V. reichenbachiana*, *V. riviniana* and *V. tricolor*.
- 244 — **virgaureae** (DC.) Lib. 3, 130; 27 (1916, 53; 1920, 38); 65 (xxxi, 368); 70 (1949, 36); syn. *Puccinia clandestina* Carm. III not common on *Solidago virgaurea*. — *zopfii* Wint. = *P. calthicola*.
- 245 **Pucciniastrum agrimoniae** Tranz. 3, 364; 54 (xiii, 503); 65 (xxxi, 427); 70 (1936, 394); 115, 43. II common on *Agrimonia eupatoria* in England and probably in Wales, but known in Scotland only near the border; II also in Ireland; III not recorded in Britain.
- 246 — **circaeae** (Thuem.) Speg. 3, 365; 48 (ix, 184); 54 (xiii, 503); 65 (xxxi, 427); 71 (xi, 48); 115, 43; 118A, 170. II common on *Circaea intermedia* and *C. luteana*; III rare. I reported by cultures on *Abies alba* in Switzerland in 1916.
- 247 — **epilobii** Oth 28 (iv, 334; ix, 140); 65 (xxxi, 428, xxxiv, 393); 3, 366 as *Pucciniastrum pustulatum* Diet.; 115, 43; 118A, 170; 54 (xiii, 503) as *P. abietichamaenerii* Kleb.; 65 (xxxi, 427). I on *Abies grandis* in south Scotland; II, III on *Chamaenerion angustifolium*, *Epilobium anagallidifolium*, *E. montanum* and *E. palustre*. Arthur and Hiratsuka agree with Grev in placing these rusts as one species. See *Uredo fuchsiae*.
- 248 — **goodyerae** (Tranz.) Arth. 65 (xxxi, 429). II on *Goodyera repens*, Moray. I and III unknown. — *pustulatum* Diet., see *Pucciniastrum epilobii*.
- 249 — **pyrolae** Diet. ex Arth. 3, 367; 65 (xxxi, 429); 115, 43. II, III on *Pyrola media*, *P. minor*, *P. rotundifolia*, *Ramischia secunda*, Salop, Yorkshire and Scotland.
- 250 **Rostrupia ammophilae** (Syd.) Wilson in 65 (xxxiii, iv). II, III on *Ammophila arenaria* and × *Ammocalamagrostis baltica*, Yorkshire and Northumberland. Some of the records of *Puccinia ammophilina* may possibly belong here.
- 251 — **elymi** (Westend.) Lagerh. 50, 178; 54 (xiii, 498) as *Puccinia elymi* Westend. II on *Elymus arenarius*, Norfolk. The II with paraphyses mentioned by E. A. Ellis may belong to another rust.
- 252 **Thekopsora areolata** (Fr.) Magn. 65 (xxxi, 429); 115, 43; syn. *T. padi* (Cooke) Grove in 3, 369. O, I on *Picea abies*; II, III on *Prunus padus*, Scotland and Yorkshire.
- 253 — **galii** (Wint.) de Toni 3, 370; 27 (lix, 314); 35 (1946, 76); 54 (xiii, 503); 65 (xxxi, 430). II, III on *Asperula odorata*, *Galium hercynicum*, *G. palustre*, *G. uliginosum*, *G. verum*, *Sherardia arvensis*, Norfolk to Scotland, etc. The correct name for this rust may be *Thekopsora guttata* (Schroet.) Syd.
- 254 — **vacciniorum** Karst. 3, 371; 65 (xxxi, 430); 70 (1936, 394); 115, 43. II widespread but not common on *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, III rare or absent; II on *Oxycoccus palustris* in Northumberland, coll. C. E. D. Smith. Jørstad (1952) uses the name *Pucciniastrum vaccinii* (Wint.) Jørst.
- 255 **Trachyspora intrusa** (Grev.) Arth. 3, 106 as *Uromyces alchemillae* Lév.; 54 (xiii, 500); 65 (xxxi, 363); 70 (1949, 36); 115, 45. II, III widespread on *Alchemilla vulgaris* agg. III of this rust were first described by Greville as *Uredo intrusa*.

- 256 **Tranzschelia anemones** (Pers.) Nannfeldt, 1939, syn. *Puccinia anemones* Pers. (1801). **28** (iv, 336); **3**, 215 as *P. fusca* Wint.; **54** (xiii, 491); **65** (xxxi, 384); **71** (xxviii, 138); **115**, 46; **118A**, 171. O, III on *Anemone nemorosa*.
- 257 — **pruni-spinosae** (Pers.) Diet. **112**, 279; **3**, 207 as *Puccinia pruni-spinosae* Pers.; **54** (xiii, 491); **65** (xxxi, 383); **71** (xl, 48); **77** (1928, 82); **79** (ii et seq.). O, I widespread on *Anemone coronaria* cult. and *A. nemorosa*; II, III on *Prunus domestica* and subsp. *insititia*, *P. spinosa*, *Prunus* spp. cult.
- 258 — **thalictri** (Chev.) Diet. **3**, 214 as *Puccinia thalictri* Chev.; **54** (xiii, 491); **65** (xxxi, 384); **115**, 46. III rare on *Thalictrum flavum* and *T. minus* subsp. *arenarium* and *montanum*, Scotland, Yorkshire, Norfolk and Kew.
- 259 **Triphragmium filipendulae** Pass. **10**, 219; **3**, 287 as a syn. of *T. ulmariae*. II, III reported on *Filipendula vulgaris*, Lewes, 1862.
- 260 — **ulmariae** (DC.) Link **3**, 287; **10**, 218*; **54** (xiii, 501); **65** (xxxi, 406); **70** (1936, 391). O, II, III widespread on *Filipendula ulmaria*.
- 261 **Uredinopsis filicina** Magn. **65** (xxxi, 438); **115**, 43; see **3**, 379. II, III on *Thelypteris phegopteris*, Argyll and Yorkshire.
- 262 [**Uredo behnickiana** P. Henn. The so-called *Hemileia* spp. of imported orchids are better placed as *Uredo* spp.; III are evidently not known. *U. behnickiana* is a prior name for *Hemileia oncidii* Griff. & Maubl., **3**, 383; **115**, 44. II on *Oncidium varicosum* from Brazil. The II spores larger than those of *Hemileia oncidii* recorded on *Oncidium* sp., **22**, Bull. 126, p. 87 may have belonged to *Uredo oncidii* P. Henn. *Hemileia americana* Massee, **3**, 381; **50**, 170, at first said to be on *Oncidium* then on *Cattleya dowiana*, may also be *Uredo behnickiana*. See *U. phaji*.]
- 263 — **festucae** DC. **27** (1921, 314; 1934, 265); **65** (xxxi, 441). II on *Festuca ovina*, Scotland (and England?). We follow Jørstad (1951) in keeping this *Uredo* distinct *pro tem*. See *Uromyces dactylidis*.
- 264 [— **fuchsiae** Arth. & Holw. **22**, Bull. 126, p. 84; **28** (xvi, 308); **112**, 288. On *Fuchsia*, Wales and Gloucestershire. This is II of *Pucciniastrum, epilobii* fide Gümman, *Phytopath. Z.* xiv. 189.]
- 265 [— **lynchii** (Berk.) Plowr. in **10**, 259; **3**, 385; **65** (xxxi, 438). II on imported *Spiranthes*.]
- 266 [— **phaji** Racib. **3**, 382 as *Hemileia phaji* Syd.; see **50**, 170. II on imported *Phaius wallichii*, Dublin and on *Phaius* sp. at Kew. This rust was possibly *Uredo behnickiana*.]
- 267 [— **plantaginis** Berk. & Br. is a later syn. of *Synchytrium plantagineum* Speg. The *Uredo* described **3**, 385 on *Plantago major* needs verification.]
- 268 — **quercus** Brond. **3**, 315 as *Cronartium quercum* Miyabe; **27** (1916, 54). II on *Quercus robur*, southern England and on *Q. ilex*, Devon and Guernsey. As Arthur points out in his *Manual*, this rust is better excluded from *Cronartium quercum* until I and III are known.
- 269 **Uromyces acetosae** Schroet. **3**, 116; **27** (1934, 267); **28** (xviii, 269); **53** (Proc. LXIII, 178); **54** (xiii, 500); **65** (xxxi, 364); **71** (xl, 47); **118**, 3. O, I, II, III on *Rumex acetosa*; II, III on *R. acetosella*.
- 270 — **airae-flexuosae** Ferd. & Winge **65** (xxxi, 366); see **3**, 265. II, III on *Deschampsia flexuosa*, Scotland and Yorkshire; also Surrey 1945, coll. Dennis.
— *alchemillae* Lév., see *Trachyspora intrusa*.
- 271 [— **aloes** (Cooke) Magn. III on *Aloe* sp. from Africa in Roy. Bot. Gard. Edinburgh.]
- 272 — **ambiguus** (DC.) Lév. **3**, 121; **70** (1949, 36); **115**, 45. II, III rare in England and Ireland on *Allium babingtonii*, *A. schoenoprasum*, *A. scorodoprasum*; on *A. ampeloprasum* in Cornwall. Near *Puccinia porri*.
- 273 — **anthyllidis** Schroet. **3**, 95; **54** (xiii, 499); **65** (xxxi, 361); **71** (xxviii, 137); **115**, 45; **130**, 60. II, III occasional on *Anthyllis vulneraria*.
- 274 — **appendiculatus** (Pers.) Unger **115**, 45; **3**, 101 as *Uromyces phaseolorum* de Bary; **22**, Bull. 126 and 139; **112**, 262. I, II, III rare on *Phaseolus vulgaris* in England; the Path. Lab. at Harpenden has one report from Cornwall and one from Devon on *P. coccineus*.
- 275 [— **ari-triphylli** (Schw.) Seeler **10**, 266 and **3**, 387 as *Aecidium 'dracontii'* Schw. I on introduced *Arisaema triphyllum*, Melbury in 1863, Kew Gardens in 1945. For some reason, only the aecidium of this American rust develops on plants imported to Europe.]

- 276 **Uromyces armeriae** Lévl. 3, 89; 48 (ix, 184); 54 (xvi, 81); 65 (xxxi, 359); 70 (1949, 35). O, I, II, III on cult. *Armeria 'grandiflora'* and *A. plantaginea* in Scotland; widespread on *A. maritima*.
- 277 — **behenis** (DC.) Unger 3, 109; 54 (xiii, 499); 65 (xxxi, 364); 71 (xlii, 48). I, III on *Silene cucubalus* and especially *S. maritima*.
- 278 — **betae** (Pers.) Lévl. 3, 113; 54 (xiii, 500); 65 (xxxi, 364); 70 (1936, 384); 112, 263. O, I, II, III common on *Beta vulgaris* subsp. *maritima* and especially subsp. *vulgaris*.
— *caryophyllinus* Wint. = *Uromyces dianthi*.
- 279 — **chenopodii** (Duby) Schroet. 3, 111; 54 (xiii, 500; xv, 371); 56 (xix). I, II, III rare on *Suaeda maritima* and its var. *flexilis*, Sussex, Durham, and especially Norfolk.
- 280 — **colchici** Massee in 14 (xxi, 6*); 3, 122; 56 (xxvii, 400*); 115, 45. Material in Herb. Kew. consists of three fragments of a leaf (or leaves), one of which bears one pustule of *Uromyces*. A slide showed the spores to be about as Massee described them. One would suspect some error, except that Massee states that the rust developed for three successive years on *Colchicum spectiosum*, and in the third year spread to *C. autumnale* and *C. variegatum*. The rust, which is also reported from Yorkshire, is much the same as *Uromyces gageae*. Massee's type in New York is evidently on *Colchicum*, fide Dr Rogers in litt.
- 281 — **dactylidis** Oth 3, 125; 54 (xiii, 501); 65 (xxxi, 367); 70 (1936, 384); 79 (ii, 30); 130, 11. O, I on *Ranunculus acris*, *R. bulbosus*, *R. repens*; II, III common on *Dactylis glomerata*. Jørstad (1951) follows Grove (27, 1934) in placing the two following as races of *Uromyces dactylidis*, all with I on *Ranunculus*.
- 282 As *Uromyces festucae* Syd. 27 (1934, 265); 130, 12. II, III on *Festuca rubra* and possibly *F. ovina*; I by inoculation on *Ranunculus bulbosus*. *Uredo festucae* (q.v.) is a similar rust but is not known to produce I or III.
- 283 As *Uromyces poae* Rabenh. 3, 127; 54 (xiii, 501); 65 (xxxi, 368); 70 (1936, 385); 130, 12. O, I on *Ranunculus acris*, *R. auricomus*, *R. bulbosus*, *R. ficaria* and *R. repens*; II, III on *Poa annua*, *P. nemoralis*, *P. pratensis* and *P. trivialis*.
- 284 — **dianthi** (Pers.) Niessl 79 (xi, 54); 85 (xli, 19); 3, 108 as *Uromyces caryophyllinus* Wint.; 65 (xxxi, 363); 80, 104*; 112, 261. II, III on cult. *Dianthus barbatus*, *D. caryophyllus* and *D. chinensis*.
- 285 — **ervi** Westend. 3, 96; 54 (xiii, 499); 65 (xxxi, 361). I, II, III not common on *Vicia hirsuta*.
- 286 [— **erythronii** (DC.) Pers. 22, Bull. 126. On *Erythronium dens-canis* from France.]
- 287 — **fabae** de Bary 3, 97; 54 (xiii, 499, xv, 209); 65 (xxxi, 361); 70 (1936, 383); 112, 262; 118, 2; 118A, 172. O, I, II, III on *Lathyrus palustris*, *L. pratensis*, *Pisum sativum*, *Vicia bithynica*, *V. cracca*, *V. faba*, *V. lutea*, *V. sativa* and *V. sepium*. The correct name for this rust may be *Uromyces viciae-fabae* (Pers.) Schroet.
- 288 — **ficariae** (Alb. & Schw.) Lévl. 3, 107; 54 (xiii, 499); 65 (xxxi, 363); 70 (1936, 384). III common on *Ranunculus ficaria*.
- 289 — **flectens** Lagerh. 3, 92; 28 (ix, 139); 54 (xiii, 499); 65 (xxxi, 360); 118A, 172; 130, 60. III on *Trifolium repens*, sometimes on *T. fragiferum*. This is a short-cycle rust near *Uromyces trifolii-repentis*. The form with O, I, III is by some called *U. nerviphilus* (Grogg.) Hotson.
- 290 — **gageae** G. Beck 3, 120; 115, 45. III reported from Yorkshire on *Gagea lutea*.
- 290a — **gentianae** Arth., det I. Jørstad, 1953: on *Gentianella amarella* agg., listed 28 (xiv, 187) as *Puccinia gentianae* Link, Worcestershire; also Hampshire, coll. M. B. Ellis in 1932 and in Herb. Kew. from Dorset. The rust on *Gentianella campestris* agg. reported 54 (viii, 680; xv, 371) from Norfolk is uncertain, as no other record of a rust on *G. campestris* is known to Jørstad or to us.
- 291 — **geranii** (DC.) Lévl. 3, 103; 48 (ix, 184); 54 (xiii, 399; xv, 371; xvi, 173); 65 (xxxi, 363); 70 (1949, 36). O, I, II, III on *Geranium dissectum*, *G. molle*, *G. pratense*, *G. pusillum*, *G. pyrenaicum*, *G. robertianum*, *G. rotundifolium* and *G. sylvaticum*.
- 292 [— **holwayi** Lagerh. 31 (N.S. xi, 820, 1879) as *Uredo prostii* Duby on *Lilium columbianum*. This in Herb. Kew. is *Uromyces holwayi* widespread in North America.]

- 293 **Uromyces jaapianus** Kleb. 28 (iv, 184 and 329; xviii, 270); 65 (xxxI, 360); 118, 2; 130, 61; 3, 93 in error as *U. striatus*; 27 (1916, 53); 28 (xxix, 168). II, III not common on *Trifolium dubium*; in Herb. Kew. on *T. campestre* from Somerset and Gloucestershire.
- 294 — **junci** (Desm.) Tul. 3, 123; 10, 132; 54 (xiii, 501); 115, 45. O, I on *Pulicaria dysenterica*; II, III on *Juncus subnodulosus* and possibly other *Juncus* spp., Norfolk, Yorkshire, etc.
- 295 — **kabatianus** Bub. 3, 104; 65 (xxxI, 363); 118A, 172. O, I, II, III on *Geranium pyrenaicum* at Edinburgh and near Reading, Berkshire (E. T. Roberts); II on this host in Cambridgeshire; two collections on *Geranium* sp. in Hertfordshire.
- 296 — **laburni** (DC.) Fuckel (based on *Puccinia laburni* DC., 1805) 27 (1934, 267) as *Uromyces genistae* Fuckel; 35 (1946, 76) as *U. genistae-tinctoriae* Wint.; 54 (xiii, 499; xvi, 80 and 173); 65 (xxxI, 362); 28 (xxix, 67) with three formae. II, III on *Genista anglica*, *G. tinctoria*, *Laburnum anagyroides*, *Sorothamnus scoparius*, *Ulex europaeus*, Norfolk to Scotland since 1934 in Herb. Kew. on broom in Kent, 1865. O, I on *Euphorbia* not found here nor obtained by inoculations.
- 297 — **lilii** (Link) J. Kunze 3, 118; 22 (Bull. 117, p. 54); 27 (1911, 368); 28 (ix, 1); 54 (xiii, 500). O, I, III on *Lilium candidum* cult., Kew, Birmingham and Norfolk.
- 298 — **limonii** (DC.) Lévl. 3, 88; 35 (1940, 28); 54 (xiii, 500); 65 (xxxI, 359). I, II, III on *Limonium vulgare* in coastal areas.
- 299 — **lineolatus** (Desm.) Schroet. 14 (xxi, 111); 3, 124 as *Uromyces scirpi* Burr.; 27 (1938, 353); 28 (xviii, 267*; xxiv, 98); 54 (xiii, 501; xiv, 188; xvi, 173); 65 (xxxii, 557); 70 (1949, 36). O, I on *Berula erecta*, *Glaux maritima*, *Oenanthe crocata*, *O. fistulosa* and *O. lachenalii*; II, III on *Scirpus maritimus*.
- 300 — **loti** Blytt 3, 94; 27 (1931, 44); 54 (xiv, 106); 65 (xxxI, 361); 70 (1936, 383); 118, 2; 130, 61. II, III on *Lotus angustissimus*, *L. corniculatus*, *L. hispidus* and *L. uliginosus*. O, I on *Euphorbia* not known here.
- 301 [— **lycoctoni** (Kalchbr.) Trott. 50, 79 'On *Aconitum*... Sometimes occurs on cultivated plants in this country.' No British specimen is known to us.]
- 302 — **onobrychidis** (Desm.) Lévl. [ex Bub.?] 27 (1919, 162); 22, *Misc. Publ.* 38 *et seq.*; 79, iii *et seq.*; 130, 60. II, III on *Onobrychis viciifolia* in England and Wales.
- 303 — **orobi** (DC.) Lévl. 3, 99; 27 (1920, 38); 65 (xxxI, 362). O, I, II, III on *Lathyrus montanus* in Scotland and occasionally in England.
- 304 — **pisi** (Pers. ex DC.) Wint. 3, 99; 22, *Bull.* 126; 65 (xxxI, 362); 112, 262; 115, 45; 118, 2. O, I reported with doubt on *Euphorbia cyparissias*; II, III rare in England on *Pisum sativum* and in Scotland on *Lathyrus pratensis*.
— *poae* Rabenh., see under *Uromyces dactylidis*.
- 305 — **polygoni-aviculariae** (Pers.) Karst. 28 (iv, 335); 65 (xxxI, 365); 3, 117 as *U. polygoni* Fuckel; 54 (xiii, 500); 70 (1936, 384). O, I rare; II, III common on *Polygonum aviculare* agg.
- 306 — **punctatus** Schroet. II on *Astragalus danicus*, Fife. (Macdonald, *Handlist of the rust fungi of St Andrews*, ?1949 as *Uromyces astragali* (Opiz) Sacc.); II, III on *Astragalus danicus* in Angus.
- 307 — **rumicis** (Schum.) Wint. 3, 114; 54 (xiii, 500); 65 (xxxI, 364); 70 (1936, 384); 118, 3. II, III common on *Rumex conglomeratus*, *R. crispus*, *R. hydrolapathum*, *R. maritimus*, *R. obtusifolius* and *R. sanguineus*.
- 308 — **salicorniae** Lévl. ex Cooke in 14 (vii, 137, 1879); 3, 114; 10, 129; 27 (1920, 38); 28 (v, 439); 54 (xiii, 500; xv, 371); 118, 3. I, II, III occasional in England on *Salicornia stricta* agg.
- 309 — **scillarum** (Grev.) Wint. 3, 120; 54 (xiii, 500; xv, 371); 57 (viii, 220); 65 (xxxI, 365); 70 (1936, 384); 79 (xi, 58); 118A, 172. III widespread on *Endymion hispanicus* and *E. nonscriptus*; on *Muscari polyanthum* cult. in Roy. Bot. Gard. Edinburgh; on *Scilla verna* in Cornwall.
— *scirpi* Burr. is antedated by *Uromyces lineolatus* (Desm.) Schroet.
- 310 — **scrophulariae** Fuckel 3, 87; 28 (xi, 16); 65 (xxxI, 359); 70 (1936, 383); 115, 45. O, I, III rare on *Scrophularia aquatica* and *S. nodosa*.
- 311 — **sparsus** (Schm. & Kunze) Lévl. 3, 111; 27 (1920, 38, 1934, 267); 28 (v, 438; vii, 7; xii, 114; xviii, 265*); 54 (xiii, 499); 65 (xxxI, 364); 118, 3. II, III occasional in England and Scotland on *Spergularia marginata*, *S. rubra*, *S. salina*; O, I also in Norfolk on *S. marginata*.

- 312 **Uromyces striatus** Schroet. **28** (xviii, 270; xxix, 167); **35** (1943, 119); **65** (xxxii, 557); **70** (1936, 383); **112**, 263; **118A**, 172; **130**, 61; not **3**, 93 which is *Uromyces jaapianus*. II, III widespread on *Medicago arabica* (first known British collection in Kent by M. Wilson in 1903), *M. hispida*, and *M. lupulina*.
- 313 — **sublaevis** Tranz., probably. III on *Euphorbia hyberna*, Kerry, Eire, coll. N. Y. Sandwith June 1952, det. R. W. G. Dennis.
- 314 — **trifolii** (DC.) Lév. **3**, 90; **54** (xiii, 499); **65** (xxxi, 360); **70** (1936, 383); **115**, 45; **130**, 60. I rare, II, III not common on *Trifolium hybridum*, *T. incarnatum*, *T. medium* and *T. pratense*. Some use the name *Uromyces fallens* (Desm.) Kern for this rust. Arthur used *U. trifolii* in a broad sense to include the next also.
- 315 — **trifolii-repentis** Liro **3**, 91; **65** (xxxi, 360); **71** (xl, 47); **130**, 61. O, I rare, II, III not common on *Trifolium repens*. See *Uromyces flectens*.
- 316 — **tuberculatus** (Fuckel) Fuckel **3**, 102; **70** (1936, 384). O, I, II, III rare on *Euphorbia exigua* in England and on *E. hyberna* in Ireland.
- 317 [— **urticae** Cooke in **14** (vii, 137); **3**, 389; **10**, 142. The type in Herb. Kew. is a fragment of herbaceous ? petiole densely covered by III of *Uromyces* sp. A note by Cooke at Kew tells us that he went to Shere, Surrey, and with Dr Capron searched the large nettle bed for more rust, but found none. In **14** (vii, 133) Cooke, nevertheless, states that 'the fact is beyond dispute that an *Uromyces* is found, late in the year, after the *Aecidium* is gone, on the stems of the nettle'. Dr Dennis deduces that the rust was probably *U. scrophulariae*.]
- 318 — **valerianae** Fuckel **3**, 86; **54** (xiii, 500); **65** (xxxi, 359); **70** (1936, 383). O, I, II, III common on *Valeriana dioica* and *V. officinalis*.
- 319 **Xenodochus carbonarius** Schlecht. **3**, 303; **65** (xxxi, 409); **115**, 44; **118**, 9. I, III on *Sanguisorba officinalis*, not uncommon in some English counties; at Melrose in Scotland.
- 320 [— **curtus** Cooke **3**, 390. The type from Manchester is one leaf or leaflet marked '? Valeriana'. It bears a few slightly roughened areas, but no rust is visible.]
- 321 **Zaghouania phillyreae** Pat. **3**, 332; see **50**, 167. O, I, II on cult. *Phillyrea latifolia* and its var. *media*, three collections in south Sussex.

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INDEX TO SYNONYMS AND OTHER NAMES ENTERED

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REVIEWS

Dispersal in Fungi. By C. T. INGOLD. (Oxford: Clarendon Press, 1953.) viii + 197 pp., 8 plates, 90 text-figures. Price 18s.

Most of the notable mycologists of the past are remembered for their major contributions to the taxonomy of fungi, for their diligence in describing new species, and many of these workers give the impression of having been more interested in herbarium specimens than in living fungi. In every generation, however, there have been a few mycologists of a 'marvelling temper' who have been fascinated by fungi as living organisms and it is to this select company that Prof. Ingold belongs. Prof. Ingold has certainly made important contributions to taxonomy, but these are an incidental result of seeking for fungi in unusual habitats and for twenty years or more he has paid special attention to mechanisms of spore discharge and methods of spore dispersal, the aspects of living fungi which he has so attractively displayed in his latest book.

The longest chapter—which occupies nearly half the book—on spore liberation, is essentially an amplification of the sections on fungi in his earlier essay, *Spore Discharge in Land Plants*, 1939 (for some years an elusive book but now again available) and this is followed by other chapters on dispersal of spores by air, by insects, by larger animals, by seeds, and by water. In conclusion there is a useful bibliography, an index, and an appendix of fungus names and if the last shows the author to have a certain insensitivity to 'correct names' and authorities it is an easily cured blemish on a stimulating little book.

G. C. AINSWORTH

The Fungi. By ERNST ALBERT GÄUMANN, translated from the German by F. L. WYND. (New York: Hafner Publishing Company, 1952.) 420 pp.; 440 text-figures. Price 72s. 6d.

English-speaking students of mycology have long had reason to be grateful to Prof. C. W. Dodge for his translation of Prof. Gäumann's *Vergleichende Morphologie der Pilze*, which has been a standard text-book of mycology since its publication in 1928. We must now make grateful acknowledgement to Prof. Wynd for this translation of Prof. Gäumann's *Die Pilze*, a revised and condensed version of his original text-book.

The emphasis of this book is on evolutionary development of the thallus (including fruit-body) and of the process of sexual reproduction. Prof. Gäumann's concept of evolutionary relationships within the fungi as a whole is given in phylogenetic scheme in the Introduction, and this is supplemented by similar presentations of mutual relationships for individual groups elsewhere in the book. To illustrate his main theme Prof. Gäumann has written an admirable account, ably translated, of the structure and life history of fungi. Four families, the Olpidiaceae, Synchronytriaceae, Plasmodiophoraceae and Olpidiopsidaceae, are placed in a separate class, the Archimycetes, as primitive, holocarpic fungi, with naked vegetative thalli, differing fundamentally in this last respect from what are described as 'true' fungi, provided with cell walls, comprising the Phycomycetes, Ascomycetes and Basidiomycetes. Discussion of the fungi within each of these classes is prefaced by keys to their component orders which conveniently summarize the taxonomic arrangements adopted. The same system is applied to certain of the orders themselves.

Lacking sexual reproduction systems, the Fungi Imperfecti receive summary treatment in an appendix of a page and a half, a feature of the book that is greatly to be deplored. It is to be hoped, for future editions, that Prof. Gäumann may be persuaded to review this important group of fungi in some detail.

In addition to a number of spelling mistakes the following errors of translation have been noted: p. 30, in the key to Phycomycetes, 'see page 23' should read 'see page 73'; p. 141, 'Plectascales' in line one should be 'Perisporiales'; p. 198, 'figure 213' (first citation) should be 'figure 212'; p. 250, 'Figure 291, 1' should be 'Figure 292, 1'; p. 342, paragraph four, 'aecidiospores' should be 'uredospores'. There are also a few

errors of fact which appear to originate in the German text, e.g. on p. 73 it is stated that asexual reproductive processes of the Zygomycetes usually resemble those of the algae, while on pp. 182 and 184 there are incorrect statements regarding the nuclear divisions within the developing ascus of *Neurospora tetrasperma*. These mistakes apart, authors and publishers are to be congratulated on the high standard of production of this book which, with its many fine illustrations and comprehensive bibliography, should be a valuable addition to the thin ranks of recent mycological text-books.

C. J. HICKMAN

Researches on Plant Diseases of the Punjab. By ABDUS SATTAR and ABDUL HAFIZ. (Sci. Monogr. no. 1, Pakistan Assn. for the Advancement of Science, University Institute of Chemistry, Lahore. Lahore: The Pakistan Times Press, 1952.) 158 pp., 77 figures, 22 tables. Price: Rs. 12.

It is thirty-five years since Edwin J. Butler published his book *Fungi and Disease in Plants*. For many years there was no revision. Then in 1949 a volume appeared, written by Sir Edwin Butler with S. G. Jones and entitled *Plant Pathology*. Originally intended as a revision, it was virtually a new book. The plant diseases, described in detail to illustrate principles, were chosen from temperate climate crops instead of tropical ones. In the same year B. B. Mundkur published *Fungi and Plant Disease*, using some tropical crops in illustration of different kinds of disease, but this book was of the nature of an elementary text-book for students.

Sattar and Hafiz, who have studied plant diseases in the Punjab for a number of years, have now written a monograph which describes their work and is intended to serve as a companion volume to Butler's book. It deals with diseases of wheat, gram (*Cicer arietinum*) and other pulses, sugarcane, cotton, rice, sorghum, oilseeds, tobacco, vegetables and fruit trees.

The authors describe a modification of Jensen's hot-water treatment for the control of loose smut of wheat which has been developed in the Punjab. This requires immersion of the wheat seed in water heated by placing it in containers in the sun. Apparently the treatment is quite effective, and it would be interesting to know to what extent it has been taken up by cultivators in Pakistan.

In connexion with the selection of varieties of crops resistant to disease it is important to determine methods by which a high degree of infection can be assured in the susceptible varieties. The writers describe work done along these lines in the case of the seed-borne smuts of wheat, oats, barley, sorghum and sugarcane. These methods involve the use of suitable temperatures, the correct soil moisture, and the right depth of sowing.

It is interesting to note that bunt is soil-borne in the hilly tracts of the Punjab, which may thus be compared with the state of Washington in U.S.A. and the province of Alberta in Canada, in both of which areas wheat bunt is frequently soil-borne and difficult to control with seed dressings.

It is interesting to note the importance of foot rot of wheat (*Helminthosporium sativum*) in the Punjab. At one time this was thought to be of little significance, but in Pakistan, as in North America, it is now recognized as a cause of reduced yields. It is interesting also to note that a sufficiency of soil moisture reduces infection. It is open to question, however, whether dressing seed with powdered copper sulphate, as recommended by the authors, effectively controls the disease. It is mentioned that control by the use of seed dressings has been studied, but no details are given.

The work suffers a good deal in the form of presentation. In particular, some of the charts are difficult to follow because attempts have been made to get too much on to them.

Although it is helpful to have an account of the research work done in recent years on the important plant diseases in the Punjab, this must remain too incomplete to form a connected story if reference is not made to work done elsewhere. It is difficult to subscribe to the view that 'our present knowledge of rusts of wheat and barley in the sub-continent of Indo-Pakistan is entirely due to the research work carried out by Mehta. . .'. This statement does less than justice to rust research workers the world over as well as to Mehta's colleagues.

The illustrations are poor. For instance, those of flag smut (p. 8) and foot rot of wheat (p. 29) are unrecognizable. Colours are poorly reproduced, e.g. fig. 24 illustrating ear-cockle of wheat and fig. 27 showing stem rust.

Despite short-comings, the monograph will prove useful as a book of reference on plant pathology studies in the Punjab. G. W. P.

Phytopathologie des pays chauds, Tome II. By L. ROGER. (*Encyclopédie Mycologique*, Tome 18. Paris: Paul Lechevalier, 1953.) 1127 pp., 201 text-figures. Price: French Fr. 10,000.

A wealth of information is contained in Dr Roger's second volume on tropical plant pathology which is divided into three main chapters. The first deals with Ascomycetes in 524 pages, the second of approximately the same extent describes diseases caused by imperfect fungi, while the third chapter is devoted to pathogenic Mycelia sterilia. Throughout the book, greater importance is naturally placed on the more serious plant pathogens, but in view of the wide tropical distribution of entomogenous fungi and sooty moulds the families Hypocreaceae, Meliolaceae and Capnodiaceae receive careful attention. The nomenclature is not always the same as that generally accepted in the British Commonwealth.

Diseases are described under systematic arrangement of pathogens and cross-references are given where both the perfect and imperfect states of the species are known. Family and generic characters, with keys, precede descriptions of specific diseases which are discussed under the same headings as noted previously. Great care has been taken in the descriptions of important species and this, together with the accompanying text-figures, should be of material assistance in diagnosing unfamiliar diseases. On the other hand, lack of illustrations of symptoms is to be seriously deplored. Selective emphasis has been placed on some crop plants; thus, for example, diseases of rice are treated in greater detail than those of other crops of equal importance.

Control measures are in general exhaustively and critically studied, although information on the inheritance of resistance and susceptibility might have been given when available. There is a misleading statement on page 1306 concerning the control of pineapple disease of sugarcane. The measures advocated by the author include *inter alia*, selection of cuttings from healthy plants and disinfection by chemicals or hot-water treatment. Actually, the causal organism, *Ceratostomella paradoxa* (de Seynes) Dade, is a soil-inhabiting fungus which does not infect standing canes, while the hot-water treatment of cane setts, which is usually applied to control virus diseases, increases the susceptibility of cuttings to invasion by the pathogen. Incidentally, no mention is made of the use of organo-mercurial compounds which have been found to be more efficient than copper fungicides in the protection of sugarcane cuttings.

In spite of its high cost, there is no doubt that Dr Roger's work when completed will be a most welcome addition to the reference libraries of plant pathologists working in the tropics. P. O. WIEHE

Census Catalogue of British Lichens. By W. WATSON. (Published under the auspices of the Foray Committee of the British Mycological Society. Obtainable from the Cambridge University Press, 1953.) 91 pp. Price 7s. 6d.

Little attention has been given to the study of lichens by botanists in this country during the last quarter of a century. A small body of enthusiasts headed by the author of this *Catalogue*, Dr Walter Watson of Taunton, has however kept the study of these interesting plants alive during that period. It is pleasing to report that there is now an increasing number of botanists becoming interested in these plants, and it is therefore a most opportune moment for the publication of this *Census Catalogue*. It fills a great need, and will no doubt further stimulate the growing interest in the lichens and their distribution in Britain.

The results of the researches into the systematics and distribution of British lichens

by Dr Watson and his 'students' during these past twenty-five years are contained in this list. The arrangement of the list is based on the author's earlier monograph 'The Classification of Lichens' (*New Phytologist Reprint*, no. 18, 1929) in which he proposed a modification of Zahlbrückner's system which is in general use on the Continent. This is a great advance in the classification used by A. L. Smith, and of course includes a considerable number of species new to Britain. The family in this list with the largest number of additions is the Usneaceae which now contains thirty-six species found in Britain against the five species described in A. L. Smith's *Monograph*. The total number of species listed for Britain is 1467, and the lichen parasites have rightly been omitted from the list. It is interesting to note that the author has included in the list such plants as *Biatorella resinæ* (Fr.) Th. Fr., *Leptorhapis epidermidis* (Ach.) Th. Fr. which Wainio and some other authors placed with the fungi. A few recent new discoveries were too late for inclusion in the list and should be added. These are as follows: *Parmelia laciniatula* (Flag.) Zahlbr. for V.C. 69; *P. arnoldii* Du Rietz for V.C. 1, 3 & 70; *Ramalina obtusata* (Arn.) Bitter for V.C. 1, 15 & 70; *Physcia wainioi* Ras for V.C. 40, 66 & 69, all of which were added to the British lichen flora by Dr Eilif Dahl, the Norwegian lichenologist. Also to be added is *Thelocarpon magnussonii* G. Salisbury, a new species described by him from the Ainsdale dunes (V.C. 59) in the *North Western Naturalist* (1953). *Leptogium rimosum* Nyl. recorded for Ireland must be deleted as this species was included through a misunderstanding.

The *Catalogue* will at long last enable private collectors and all institutions with lichenological collections to put their herbaria into order and thus facilitate reference. It is hoped, too, that the many collections which have been neglected owing to the lack of workers will be re-arranged and re-studied. Many new records will undoubtedly be revealed. It seems highly important that this *Census Catalogue* of Lichens which is the first ever published for Britain should be kept up-to-date by the addition of all new records, and the old and doubtful ones should be investigated. A very helpful list of lichenological papers is included, together with a list of new combinations. The *Catalogue* is well printed, but it is a pity that a better quality of paper has not been used for it as writing in ink shows through the pages. Students are advised to have it interleaved and re-bound as undoubtedly they will wish to note additional records.

F. A. SOWTER

Flore Analytique des Champignons Supérieurs (Agarics, Bolets, Chanterelles) comprenant les espèces de l'Europe occidentale et centrale... By R. KÜHNER and H. ROMAGNESI. (Paris: Masson et Cie. 1953.) Pp. xiv + 556, 677 text-figures. Price: French Fr. 7010 (7970 bound in cloth).

This important and eagerly awaited book is nominally a companion volume to Bourdot and Galzin's well-known work on the Aphyllophorales, so that 'les Mycologues puissent couvrir avec ces deux ouvrages la quasi totalité des Basidiomycètes supérieurs, à la seule exception des Gastéromycètes'. In fact, the two works have little in common. That of Bourdot and Galzin is a formal flora on classical lines, with adequate author citations and indications of the material studied. The present book is primarily a collection of keys to genera and species, with only skeleton diagnoses, and almost lacks documentation, though there is an ingenious system of citing approved illustrations and descriptions. In adopting this style the authors were no doubt influenced by a praiseworthy desire to comprise the text within a single volume, producible at a reasonable price, but it may be doubted if any of the new names and new combinations proposed in it are validly published under the International Code of Botanical Nomenclature as amended at Stockholm in 1950. Our authors, however, will not be troubled by that consideration for they have supreme contempt for 'les Règles des Congrès internationaux... faites par et pour les Phanérogamistes', or, at least, for those who attempt 'appliquer à la lettre de telles règles à une science encore aussi mouvante que celle des Champignons supérieurs'. The force of the last argument is rather lost when one turns to the text and finds the authors have as a rule adopted wide generic concepts, much nearer to the original subgenera of Fries than those found in most continental floras of recent years.

These deviations from the classical mould do not make Kühner and Romagnesi's work of negligible significance. On the contrary, it is the most important detailed treatment

of the european Agaricales since *Hymenomyces europaei* appeared in 1874, especially since the text is extremely practical, based to quite an exceptional degree on personal observations and experience. In this it forms a complete antithesis to Rea's *British Basidiomycetae*, justly dismissed with a contemptuous reference in a footnote to p. vii as 'un amalgame peu heureux des descriptions macroscopiques de Quélet avec les indications microscopiques de Ricken'.* No agaric flora is likely to be foolproof, but as far as we have tested them the keys are remarkably sound and easy to apply. Particularly successful are those to the large and complex genera *Inocybe* and *Cortinarius* and to the agglomerations listed under the names '*Drosophila*' and '*Geophila*'. The *Cortinarius* key in particular is a masterpiece, with its marshalling of nearly 300 species in fifty-four groups and its numerous helpful cross-references. Readers will be thankful to find they are no longer required to distinguish at the outset between *Inoloma* and *Dermocybe* or between *Telamonia* and *Hydrocybe*. The key to the comprehensive genus here misnamed '*Rhodophyllus*' seems rather less easy to follow.

If, then, one judges a Flora by the facility with which one can arrive at the same name for a specimen as might have been applied to it by the authors of the book, then the present work is a brilliant success. For so much we should, indeed, be thankful, and so far the authors are entitled to our congratulations and our gratitude. Unfortunately a student who buys a book of this size and quality is entitled to ask still more. He may justly expect to arrive at the legitimate specific epithet for his fungus and to find it in a combination under a genus tenable under the International Code of Nomenclature and hence internationally acceptable. Here our authors fail him, not in ignorance but of set purpose. They reject the Code of Nomenclature, so laboriously built up and consecrated by international agreement, and on page xiii of their preface they erect in its place a new code under which the names printed in their text have been chosen.

Because of the importance both of the book itself and of the principle so boldly enunciated, that an author is entitled to invent a nomenclatorial code of his own to suit his own ideas of the small group of organisms in which he has specialized, it is necessary to consider this new proposed Code in some detail.

Article I states the starting-point of Agaric nomenclature to be Fries's *Epicrisis*, 1836-8, instead of the *Systema mycologicum*, 1821, 'qui n'est qu'un travail de débutant'. The objection is frivolous and indeed irrelevant. The change of date seems to serve no nomenclatorial purpose beyond eliminating S. F. Gray's *Natural Arrangement*, 1821, as a starting-point of agaric names. Both Donk and Singer have shown that recognition of this book does not involve any insuperable difficulty in suitably typifying the genera concerned and the proposed introduction of yet another starting-point date into mycological nomenclature is highly objectionable. Moreover, the date is not even precise, nor are the authors consistent in its adoption. Thus, in the text we find, for example, *Naucoria* Fries 1821, *Hebeloma* Fries 1821, etc. According to their own rules these names have no standing as their date is pre-starting-point. In fact, of course, they do not exist at all, for Fries never recognized genera with such names, which should be cited as *Naucoria* (Fr.) Kummer 1871, *Hebeloma* (Fr.) Kummer 1871, etc.

Article 2 adopts the so-called 'residue method' in typification of generic names, but the authors decline to apply their own rule in the cases of *Polyporus* and *Agaricus* 'qui ont fourni au langage courant des mots commodes à employer dans un sens large (Agaric, Polypore, etc.)'. Here, again, the Code of Nomenclature, intended for all nations and all languages, is made subservient to the exigencies of the French tongue. This is a French Flora but the binomial names adopted in it and the rules by which they are selected should be equally applicable from Tokyo to Tucuman. By the same principle one would expect *Boletus* to disappear also, since 'Bolets' is a common word 'au langage courant', but *Boletus* is retained because the authors treat *Ixocomus*, *Xerocomus*, *Tubiporus* and the like as subgenera only. Presumably those who raise them to generic rank will be expected to eliminate the name *Boletus*.

Article 3 states that when several pre-existing genera are united, or sections from different genera, the united genus should bear the name of the oldest of its components. But, when convenient, they will not apply this rule to names of Friesian origin but will adopt instead an entirely different name, if one is available published prior to 1900. The

* For 'Quélet' read 'Fries' and the comment, though biting, becomes fair enough.

† *Sic*, perhaps 1836 is meant.

only purpose of this evasion appears to be to 'legitimize' certain names proposed by Quélet in 1886 and since forgotten. Thus we have the equations:

Stropharia Fr. 1863† – *Psilocybe* Fr. 1821 – *Hypholoma* Fr. 1821 = *Geophila* Quélet 1886;
Pholiota Fr. 1821 – *Flammula* Fr. 1821 = *Dryophila* Quélet 1886;
Psathyrella Fr. 1836 – *Psathyra* Fr. 1838 – *Pluteopsis* Fayod 1889 – *Lachrymaria* Pat. 1887
 = *Drosophila* Quélet 1886.

This is a particularly flagrant case because *Psathyrella* (Fr.) Quélet 1872 has already been emended by others to cover most of the ground. Presumably it is this Article 3 which explains the equation *Eccilia* (Fr. 1821?) – *Claudopus* (Fr.?) – *Nolanea* Fr. 1821 – *Entoloma* Fr. 1836 – *Leptonia* Fr. 1821 = *Rhodophyllus* Quélet 1886, though to save this illegitimate name Article 5 has to be invoked as well. It may be noted that all these names of Friesian origin, except *Stropharia*, *Psathyrella* and *Claudopus*, were raised to generic rank by Kummer in 1871.

Article 4 states that the rule of priority will be followed in choice of generic names except that, because of the importance of the works of Quélet, Fayod and Patouillard, choice among non-Friesian generic names prior to 1900 will be made of that which 's'adapte mieux (ou le moins mal) à la coupure considérée'. One law for Fries, another for French authors, and the rule of priority for the barbarians. Presumably it is this chauvinism which accounts for the adoption of *Mucidula* Pat. 1887 in place of *Oudemansiella* Speg. 1881, but as the taxon concerned ranks here only as a subgenus no great harm is done.

Article 5 avoids using generic names pre-occupied in other fields of botany but the authors decline to apply the rule to generic homonyms published between 1836 and 1900 inclusive. They are thus enabled to use, for example, *Omphalia* and *Rhodophyllus*, though the latter is not of Friesian origin.

Serious objections can also be raised to some of the specific epithets selected, though these do not involve the same important issues of principles as do the generic rules. Thus it is hard to see how the authors justify the name '*croceus* Bull.' for the species of *Hygrophorus* called *constans* by Lange, the legitimate epithet for which appears to be *langei* Kühner.

Authors are, of course, free to form and express whatever opinions they choose and, as the rejection of the International Code is explicitly and openly made, no one can justly complain that he has been misled by Kühner and Romagnesi's book. Nevertheless, one feels that the introduction of a set of heterodox rules, complete with exceptions which allow the authors in practice to adopt any name they please, with no guarantee that the same rules in other hands will lead to the same conclusion, is highly objectionable in a book of this kind. This claims to be a definitive Flora intended for general use throughout western and central Europe, and few of those into whose hands it will fall will be in a position to judge the issues for themselves. On the contrary, its excellence as a determinative manual will inevitably lead to the gradual adoption within the area served of the illegitimate names favoured by its authors. These, they must know, would stand little chance of approval at any international congress but in due course it will be possible to plead that, like *Rhodophyllus* to-day, they have become hallowed by 'usage', and to this extent the authors may be held guilty of something approaching sharp practice in nomenclature. Its appearance will tend to intensify and perpetuate the regrettable modern trend towards adoption of mutually unintelligible sets of names in France with its satellites on the one hand, and the rest of the world on the other. For this, in spite of their brilliant analysis and critical diagnoses, the authors will stand condemned at the bar of posterity.

R. W. G. DENNIS

'*Polyporaceae*'. *Contribuição para a sua Bio-taxonomia*. By J. PINTO-LOPES, in *Memórias da Sociedade Broteriana*, 8, 1–196, 29 figures, 1952.

The purpose of this work is to 'outline a new method of classification' of the *Polyporaceae*. It is based on a study of about ninety European species and is supported by a fairly extensive review of pertinent literature. The new classification depends on a distinction between primary, secondary and tertiary hyphae, which no systematist, apparently, has previously grasped. 'The characters of the secondary and tertiary hyphae

taken together . . . allow the division of the family in subfamilies' (p. 178). Seven subfamilies are defined with twenty-one genera variously emended, one new genus (*Trametella*, p. 164), and others subduced as synonyms. The classification differs in several respects from those of Patouillard, Bourdot, Donk, Pilát, Singer, Cunningham and others, but is it any better? I propose to show that it is no better, and that it is but another 'juggle', as Lloyd would have said.

In the first place, a large cosmopolitan family cannot be re-classified on ninety European species. A century ago there was no alternative. Now there are mighty collections, and, had Pinto-Lopes studied nine hundred species of these, he would have learnt that most of his generic and subfamily distinctions broke down with extra-European floras. The common *Polyporus zonalis* unites his Cladomeroideae with his Mensularioideae; the common *P. (Amauroderma) rugosus* unites his Trametoideae with Phaeochroideae; and the host of xanthochroic polypores amalgamates his definitions of *Phaeolus*, *Phellinus*, *Polystictus* and *Xanthochrous*. On the other hand, *Trametes*, as used by Pinto-Lopes, is of the order of a subfamily.

Secondly, what are these categories of hypha? They are, according to Pinto-Lopes, three steps in the development of the mycelium. Primary hyphae are the haploid, or non-diploidized, hyphae arising from heterothallic spores. Secondary hyphae are the thin-walled and colourless primary hyphae diploidized, or the hyphae arising from a homothallic spore. Tertiary hyphae are secondary hyphae that have enlarged, or become thick-walled or pigmented. These alterations are well-known. What systematists have not done is to number them. I find the method illogical and in conflict with that very priority which Pinto-Lopes endeavours to establish. What is primary must be first or import most. Yet, homothallic species have no primary mycelium. Their first mycelium, of primary importance for the development of the fungus, is Pinto-Lopes's secondary. Tertiary hyphae differ in quite other and unrelated ways, not comparable with the nuclear distinction between primary and secondary. This method of numbering suggests calling the ground-floor of a house the first or the second according to whether the occupants are single or married, and referring to all other constructions, from attic to cellar, lift and outhouse as the third floor, regardless of the occupants. Haploid fruit-bodies of heterothallic species, which develop sometimes in culture, must be composed of primary hyphae, but they will show tertiary characters as inflated cells, thick walls and pigmentation. The terms are not applicable.

In deriving this use of primary, secondary and tertiary from Falck, Bensaude and others, Pinto-Lopes overlooks with them the distinction between primary and secondary mycelia made by de Bary in 1884, and adopted by Fayod in 1889. I know of no earlier use of the expressions and I have always regarded their use for non-diploidized and diploidized mycelia as an error. Now that this error is to be made into a new morphological approach to fungus fruit-bodies, it must be exposed. I would mention, too, that Pinto-Lopes misuses the word hymenophore for sporophore, carpophore or fruit-body, again in contradiction of de Bary (1886, 1884) when he laid the foundations of mycological morphology.

Now, how can one decide if a hypha, that is a file of cells, is secondary, using Pinto-Lopes's meaning, or tertiary? It is thin-walled: some of its cells then inflate, or become thick-walled or coloured: and then they branch to form thin-walled laterals that may or may not undergo the same changes. Is it only the apical cell, or terminal row of cells, that is secondary for a short time before it matures? Applying the same idea to green plants, the young and small-celled meristematic tissue is the primary, and the mature tissue with large, thick-walled and, maybe, coloured cells is the secondary, but this is not botanical usage. Why should fungi be excepted? The maturing of cells is not a transition from a primary to a secondary category. The process is correctly illustrated by de Bary's distinction between the primary mycelium that forms the fruit-body and the secondary mycelium added to the primary from the fruit-body. Similarly, Pinto-Lopes's use of primary, secondary and tertiary for the septa of his respective mycelia is a misapplication of the words. In all cases the septa are formed in identically the same way. If the organ on which they occur is to define them into categories, then the septa of haploid and diploid plants, in general, will have to be called primary, secondary and tertiary (in this case for their true secondary tissue). I have, however, in my monograph on the clavarias previously used the expression 'secondary septa' in the obvious sense of

those septa developed in a cell after its delimitation by primary septa. Pinto-Lopes sets aside this clear priority without explanation.

As an example of his tertiary mycelium, Pinto-Lopes gives the thick-walled setae. They are, of course, thin-walled and, therefore, secondary to begin with, as with all his tertiary constructions. But, in some cases, the apex of the seta remains thin-walled, uninflated and colourless, so that the distal half of the seta is secondary and the proximal tertiary. If the same reasoning be applied to basidia, then the young and uninflated basidia are secondary and the mature, inflated basidia are tertiary, while in Cunningham's honeycomb-type the basidia are doubly tertiary for an additional reason, that of wall-thickening, in their proximal part. If the terms are applied to the spores, thin-walled and hyaline spores will be primary if heterothallic, and secondary if homothallic, but coloured or thick-walled spores will be tertiary, whether homothallic or heterothallic. Obviously the construction of fungi cannot be fitted into a rule of one-two-three, which is why systematists had not pursued the idea.

More surprising is Pinto-Lopes's failure to distinguish between the hyphae of the mycelium proper, or vegetative hyphae, and those of the fruit-body. That they are conrescent, trophic, not trophic, and tissue-building seems not to matter. Indeed, Pinto-Lopes does not realize what de Bary so clearly explained, that the fruit-body is developed from conrescent, reproductive hyphae growing at their thin-walled tips in a 'fungus meristem'. Thus it is, I believe, that Pinto-Lopes is unable to follow the anatomical work that Cunningham and I have been doing on polypores and other fungi, considering it erroneous in no uncertain terms (pp. 144-149) and discarding it as well as Cunningham's classification. The following examples will show that this new method of classification fails completely to penetrate the problem of the polyporaceous construction:

Melanopus squamosus (p. 102): the wide 'tertiary hyphae' are thick walled segments of generative hyphae: the narrow 'tertiary hyphae' are binding hyphae of limited growth (Cunningham's Bovista-hyphae).

Coriolus versicolor (p. 96): the 'tertiary hyphae' are the skeletal hyphae and their mediate parts, the copious binding hyphae being entirely overlooked.

Ganoderma lucidum (p. 97): the hyaline 'tertiary hyphae' are binding hyphae, the coloured ones being skeletal hyphae, both of very limited growth with free ends in the tissue (unnoticed by Pinto-Lopes).

Bjerkandra, *Heterobasidion* and *Trametes* are distinguished by Pinto-Lopes on whether the 'tertiary hyphae' are septate or not and whether the hyphae are clamped. The first is monomitic, the second is dimittic with skeletal hyphae, and the third is trimitic.

Cladomeris contains both *Polyporus giganteus* (monomitic) and *P. sulphureus* (dimittic with binding hyphae), without the author realizing this great difference.

Ganoderma contains both *G. applanatum* and *Fomes fomentarius*, though their hyphae are as different as their spores.

I conclude that Cunningham and I can find much more in polypores than there is in this new classification. If the author had traced the fragments of hyphae, which he uses as illustrations, to their origin in the growing points, he would have discovered the skeletal and binding hyphae which he rejects.

E. J. H. CORNER

1. The reviewer's declared purpose was to show that my 'classification' is no better than those of Patouillard...Cunningham and others, and that it is but another 'juggle'. One gathers that there is little intention of reviewing my paper. From the very beginning, the reviewer *misunderstands the aims pursued and the methods used in my work. He misinterprets the terminology I use, showing at the same time rather surprising ideas on the life-cycles of fungi.* Throughout his article, he enunciates as an axiom that I overlook, misuse and fail. My great failure, it seems, is that I do not follow his and de Bary's terminologies and interpretations. His final conclusion is that he himself and Cunningham can find much more in polypores. The form he uses and his reasonings leave little room for controversy and may be rather misleading to the unspecialized reader. Therefore I feel forced to summarize my own paper, answering his criticisms as the opportunities arise.

2. The purpose of the work was to test the value of experimentation in the taxonomy of the Polyporaceae. Indeed, notwithstanding the general acceptance of the modern

biological trends in taxonomy, attempts have not yet been made to confirm experimentally the morphological and anatomical basis employed by the taxonomists of the Polyporaceae. Keeping this in mind, critical reviews on life cycles, genetics, sexuality, mycelial development, antibiosis and culture characters were made. The possibility of applying this knowledge to taxonomy and systematics was assessed. It was then concluded that at present it is still insufficient for justifying any of the existing systems or indeed for developing a new one. A bibliographic synthesis on anatomy and its taxonomical application, and on the many existing hyphae terminologies was made.

3. In what concerns personal research, I tried to compare the hyphae of fruit-bodies with those grown in cultures in order to find out: (a) the morphological kinds of hyphae which are common to both conditions; (b) the constancy of their characters; and (c) their origin and development (differentiation and regression). On this basis, those hyphal characters which could be used in taxonomy were selected. *This work was carried out with a sample of species (about ninety) I considered representative of the group. For those familiar with laboratory work it is obvious that it is not practical to work with hundreds of species (fruit-bodies and cultures), especially in a preliminary study.*

4. Concerning the hyphal terminology to be adopted, I felt it necessary to attempt some order in the present confusion. In order to carry this out, I established that the terminology employed should be equally applicable for describing life cycles, fruit-bodies and mycelia growing either on artificial or on natural substrata. Falck's terms, primary, secondary and tertiary, the first two of a generalized and justified use among biologists, fulfilled this condition and therefore were preferred after redefinition. I redefined them, taking into account the present knowledge on cytological, morphological and developmental characters. *I am not responsible for, and I certainly disown, the definitions attributed to me by the reviewer. When the reviewer states that the terms are not applicable and the method is illogical, and, accordingly, when he denounces my mistakes and errors, it must be understood that he is referring to his own misinterpretations and erroneous definitions of terms I used. The same applies to my failing to realize 'de Bary's clear explanation' and to misuse of words: Whenever I prefer any term or expression I give my reasons for it. I did not follow the reviewer's hyphal terminology because it does not stand to critical analysis; his terms are so imperfectly defined as to need continuous amendments, and they are not clearer than their existing synonyms. On the other hand, Falck's 'error' of misusing de Bary's previous numbering, has been repeated in the vast literature of the last thirty years, so that to-day, as far as I know, the reviewer is the only supporter of de Bary's original meaning. I made no claim to priority of the use of terms. I simply adopted those appropriately expressing the accepted concepts of modern mycology. While reviewing the history of terminology, I assigned to Corner his true chronological place. I did not accept his priority in the idea that fruit-bodies may be formed by one or more types of hyphae. But I made clear in my paper that he has the priority in submitting the fruit-bodies to a 1-2-3-mitic rule. On the other hand, I do think Falck has the priority as to the statement that the 'vegetative mycelium' is formed by different types of hyphae, constituting several systems defined by their structure and function. I did not attribute to the reviewer the 'clear priority' in the numbering of septa, because it had been done before him, in another meaning. Having studied the kinds of septa of the hyphae, I showed that, as it was already known, they are not always formed in the same way, and that the same types of septa can appear in different types of hyphae.*

5. Falck's concept of primary, secondary and tertiary hyphae representing successive stages in mycelial development has been experimentally proved. In this respect I investigated the general aspects of development from secondary to tertiary stages and its different forms. I found that natural fruit-bodies are always formed by secondary and tertiary hyphae which I also observed in cultures of mycelia isolated from fruit-body flesh. Cultures also revealed the main types of secondary and tertiary hyphae in the whole of the group studied, and the relative importance of their characters. Thus among the many aspects presented by the hyphae in the fruit-bodies, I determined those which always subsisted in cultural conditions.

6. After having described the main types of hyphae, their constancy and origin, I offer uniform descriptions of fruit-body flesh for each one of the species studied. As I stated, *I was not concerned in giving detailed descriptions for each species, but in recording only those characters which seemed to me significant of possible relationships. Having overlooked my actual purpose, the reviewer derisively writes that Cunningham and himself 'can find much more in poly-pores' and that I have left unnoticed some characters and differences. I did not discard the facts*

revealed by his and Cunningham's investigations, as far as they do not collide with factual evidence, nor did I reject the existence of 'skeletal' and 'binding' hyphae. Their terminologies and interpretations were discussed and, as a result, were not accepted.

7. I discussed the taxonomical value of the different fruit-body characters and then proceeded to classify them (under 'Foundations of classification'). Hyphal characters, as I considered them, as well as characters of fruit-body surface (after Lohwag's terminology) and of flesh texture (following Ames) were given greatest weight. Taking into account these foundations, an analytical review of the principal systems of classification was made. Cunningham's system was discussed with greater detail and considered inconsistent.

8. Lastly the taxonomical consequences of accepting the proposed foundations were examined, and an outline (ensaio, esboço, ébauche, Grundlagen) of a methodic arrangement then presented. Species showing identity of secondary and tertiary hyphae were grouped. Differences in the characters of wall-thickness and width of the hyphae, together with those of the surface and those of flesh texture, were used for subdividing those groups. The former groups were taken as subfamilies and their subdivisions as genera. Subfamilies and genera were enunciated in an order according to the consideration that the presence or absence of clamps and the mode of differentiation of hyphae represent steps of evolution. *The positions assigned to two subfamilies were declared 'incertae sedis'*. Fortunately Corner knows one species which strengthens the position assigned to one of them, and he mentions another species which unites two other suggested subfamilies. As to the genus *Ganoderma*, adopted in the meaning of Ames, I suggested that, according to hyphal differences, *G. applanatum* and *Fomes fomentarius* should be separated in two subgenera (Cunningham considered *Ganoderma applanatum* in the same genus as *Polyporus gilvus* though their hyphae, surface, texture and colour of flesh are as different as their spores). According to the reviewer, my 'new method of classification fails completely to penetrate the problem of the polyporaceous construction'; to prove this, he presents some examples from which no one can conclude anything else but that we are using different terminologies.

9. My work does not, by any means, deal with a reclassification of a large cosmopolitan family. The arrangement given represents an application, to a sample of species, of my proposed taxonomical foundations. I did not attempt a definition or an identification of species, being concerned only in showing the possibility of using a new basis for establishing higher taxonomic groups. No new names were proposed for the species mentioned, thus showing the character of my work.

10. Well-founded criticism is welcome and further research most desirable. My paper is principally a provocation to discussion and an invitation to develop the manifold lines of work there suggested.

J. PINTO-LOPES

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